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Estimation of Functional Responses of Predators on Juvenile Salmon

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PETERMAN, R. M., AND M. GATTO. 1978. Estimation of functional responses of predators on juvenile salmon. J. Fish. Res. Board Can. 35: 797–808.

Several studies have shown that predators can eat large portions (up to 85%) of emerging salmon (*Oncorhynchus* spp.) fry populations. To understand salmon population dynamics and the effect of salmon enhancement projects, it is necessary to determine how present predation mortality varies with prey density. To predict the shape of this relation outside the range of past observations, we must examine the basic components of the predation process, the functional and numerical responses. A review of past, sparse data on the functional response component shows that predators of salmon fry and smolts were mostly not being saturated (i.e. maximum attack rates were not being achieved) at high prey densities. A method to estimate functional responses from certain types of existing field data is derived and applied to Hooknose Creek pink salmon (*O. gorbuscha*) and chum salmon (*O. keta*) information. Results from 7 out of 9 yr corroborate earlier observations that predators are normally operating on the low end of their functional response curves and are therefore capable of causing high mortality on larger prey populations. Also, competition among predators is demonstrated to be significant, resulting in changes in slopes of functional responses. More experimental studies of functional responses are needed, and such research should be carried out in conjunction with perturbations in salmon fry abundance which will result from enhancement projects.

Key words: salmon fry, predation, freshwater survival, enhancement, functional response, predator competition

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PETERMAN, R. M., AND M. GATTO. 1978. Estimation of functional responses of predators on juvenile salmon. J. Fish. Res. Board Can. 35: 797–808.

Plusieurs études ont démontré que les prédateurs peuvent manger des portions considérables (jusqu'à 85%) des populations d'alevins de saumons (*Oncorhynchus* spp.) au moment de leur émergence. Afin de comprendre la dynamique des populations et l'effet des projets de mise en valeur du saumon, il est nécessaire de déterminer comment la mortalité actuelle par prédation varie avec la densité des proies. Afin de prédire le caractère de cette relation en dehors de l'éventail des observations passées, il nous faut examiner les composants de base du processus de prédation, ainsi que les réponses fonctionnelles et numériques. Si l'on passe en revue les quelques données antérieures sur le composant réponse fonctionnelle, on constate qu'il n'y avait généralement pas saturation des prédateurs de jeunes alevins et de smolts de saumons (i.e., les taux maximums d'attaques n'étaient pas atteints) à de hautes densités de proies. Nous établissons une méthode permettant d'estimer les réponses fonctionnelles à partir d'observations existantes cueillies sur le terrain et appliquons cette méthode aux saumons rose (*O. gorbuscha*) et keta (*O. keta*) du ruisseau Hooknose. Les résultats de 7 sur 9 a confirment des observations antérieures à l'effet que les prédateurs fonctionnent normalement à l'extrémité inférieure de leurs courbes de réponses fonctionnelles et sont donc capables de causer une forte mortalité dans les grandes populations de proies. En outre, on démontre qu'il y a une importante compétition entre prédateurs, entraînant des changements dans les pentes des réponses fonctionnelles. On a besoin de plus d'études expérimentales des réponses fonctionnelles; une telle recherche devrait être poursuivie de concert avec des perturbations dans l'abondance des alevins de saumons résultant des projets de mise en valeur.

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IT has been recognized for many years that predation can be a very significant mortality agent on juvenile salmon (*Oncorhynchus* spp.) (Brett and McConnell 1950; Foerster and Ricker 1941; Johnson 1965; Neave 1953; Ricker 1941, 1962). Several studies show that up to 55–85% of salmon fry or smolts can be removed by predators such as coho salmon (*O. kisutch*) smolts, sculpins (*Cottus* spp.), trout (*Salmo* spp.), or char (*Salvelinus* spp.). These studies were done for predation in freshwater (Foerster 1968; Hunter 1959; Neave 1953) and in early marine life (Parker 1968, 1971).

For two major reasons more needs to be learned about the relation between percent predation mortality and the abundance of juvenile salmon. First, a complete understanding of salmon population dynamics and setting of "optimal" escapements must take into account the dynamic nature of the predator–prey interaction. Assuming a fixed percent predation mortality would be misleading. Second, British Columbia, Alaska, and Washington are presently embarked on large-scale enhancement programs designed to at least double current salmon production by increasing abundance of juvenile salmon through controlled rearing conditions. One major question that must be asked is how the predation mortality on salmon will be affected by increased numbers of prey. If predators are presently far from being saturated (i.e. if attack rates are not at their maxima), if predators grow faster in response to increased food supply, or if they continue to consume large portions of the juvenile salmon population, then results of enhancement may not be as great as anticipated.

Overview of Existing Data and Theory

DATA

Neave (1953) and Hunter (1959) demonstrated from field experiments that there are situations where the percent predation mortality decreases as salmon fry numbers increase (Fig. 1 and 2). This inverse relation is the result of the swamping effect on predators caused by large prey populations. Neave termed this inverse relation between percent predation mortality and prey numbers "depensatory" mortality (as opposed to compensatory) and this concept has subsequently played an important role in salmon biology.

However, other data from Neave (1953) for another stream do not clearly show this swamping effect (Fig. 3). In addition, each data point in the first three figures is for a different year and is therefore most likely associated with different predator population sizes. To predict predation mortality for fry and smolt densities outside the range of past observations, it is necessary to obtain a more complete picture of changes in predation numbers and their rate of consumption.

THEORY

This picture of overall predation mortality requires an investigation of what Solomon (1949) originally called the functional and numerical responses of predators, and which Holling (1959a) termed the basic components of the predation process. The functional response describes the number of prey eaten per predator per unit time in relation to the prey density, and the numerical response describes how the number of predators varies as a function of some measure such as prey density. This numerical response can arise quickly through aggregation of predators or more slowly through altered reproductive success.

There is an extensive empirical as well as theoretical literature dealing with functional and numerical responses, especially in the field of entomology. This literature contributes three main points of relevance to salmon managers and biologists. First, there are several

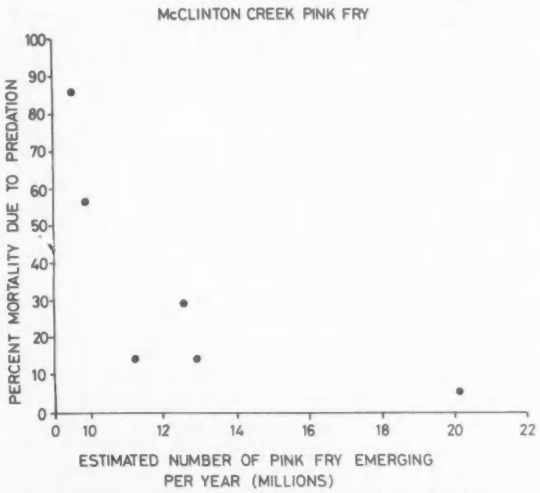

FIG. 1. Estimated yearly pink salmon (*Oncorhynchus gorbuscha*) fry predation mortality in relation to pink fry emergence, for McClinton Creek, B.C. (after Neave 1953).

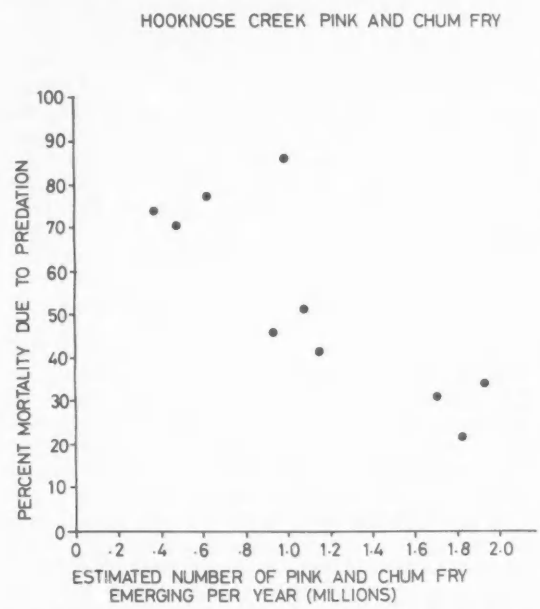
HOOKNOSE CREEK PINK AND CHUM FRY
PERCENT MORTALITY DUE TO PREDATION
ESTIMATED NUMBER OF PINK AND CHUM FRY EMERGING PER YEAR (MILLIONS)

FIG. 2. Estimated yearly pink and chum salmon (*O. keta*) fry predation mortality in relation to total pink and chum fry emergence on Hooknose Creek, B.C. (after Hunter 1959).

different classes of functional and numerical responses that can be exhibited by predators, each class having its own characteristic effect of changing prey numbers on percent predator mortality. Second, certain types of predators (e.g. vertebrates) generally show only a subset of these possible types of responses. And third, each type

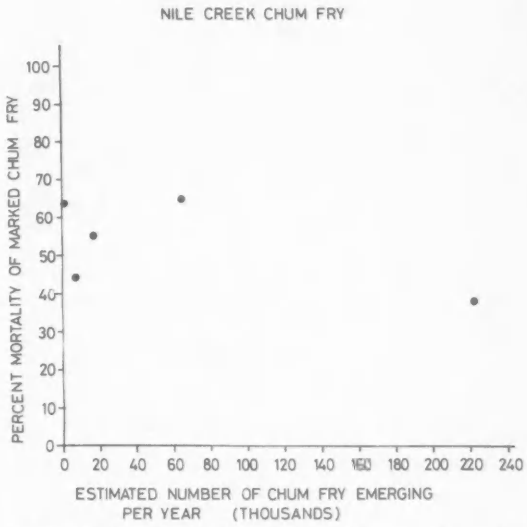

FIG. 3. Estimated yearly chum salmon fry mortality in relation to chum emergence on Nile Creek, B.C. (after Neave 1953).

of functional and numerical response results in a different stability characteristic for the predator–prey system. Let us examine these three points in more detail.

Figure 4 shows examples of four types of functional responses, three of which were described by Holling (1959a, 1965), and the fourth arising from subsequent studies that show the existence of "refugia," characteristics of behavior or environment that prevent predators from finding prey below certain prey densities. Note that each type of functional response asymptotes at some level, because of predator gut capacities or handling time constraints, and each creates a different-shaped percent mortality curve (Fig. 4B). Note also that variance in the data may obscure the underlying relationship if data are plotted as in Fig. 4A, but we can distinguish between the different-shaped relationships more easily by plotting the same data as percent mortalities; the curves have more unique shapes (see Fig. 4B). The salmon biologist should know the shape of these percent mortality curves so that he can determine at what population sizes of juvenile salmon there will be a significant drop in mortality due to swamping of predators. If predators show a Type III response as in Fig. 4B and if present prey densities are so low that predators are operating on the low end of the functional response curve, then salmon enhancement programs that boost production to, say, 20 prey density units will result in higher percent predation mortality. Salmon managers who alter the timing of fry release from enhancement facilities also need to know the threshold fry density, on a daily basis, that is necessary to achieve a significant swamping effect. As a predator grows in body size the asymptote of its functional response will increase because of larger gut capacity, faster swimming speed, etc. (Murdoch 1973). Therefore, caution should be exer-

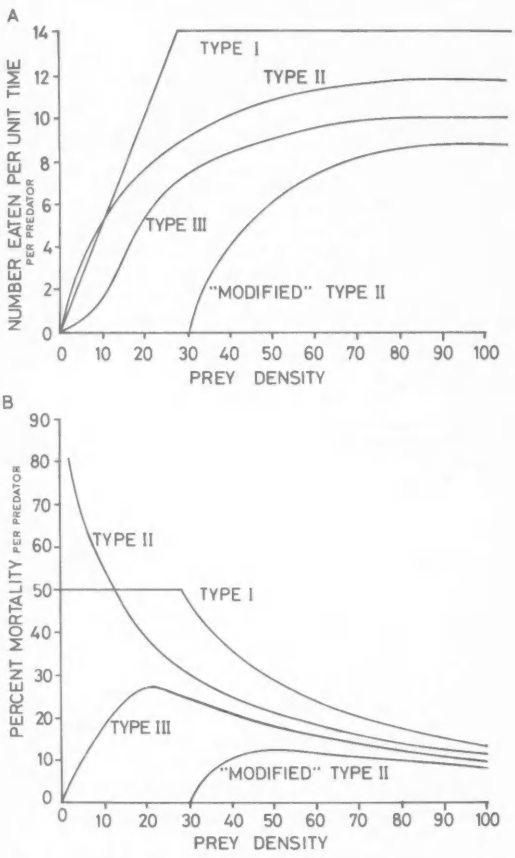

FIG. 4. Shapes of different types of hypothetical functional responses (A) and their corresponding percent mortality curves (B) (Types II and III redrawn from Holling 1959a).

cised when extrapolating a measured functional response to a later point in time.

It would be sufficient to measure only functional response relations if predator numbers were constant. But of course they are not, and the total number of prey eaten is a product of the number eaten per predator per unit time (described by the functional response) and the total number of predators present each time unit. The numerical response describes the latter quantity and again extensive literature indicates that the form of this response can vary radically (Beddington et al. 1976; Hassell et al. 1976; Holling 1959a). On a short time scale, predators can aggregate to an area where prey numbers are high or can leave when prey decrease (Hassell et al. 1976; Holling 1959a; Hunter 1959), giving a numerical response that has a shape similar to Type II or III functional responses. On a longer time scale, predator reproductive success may be directly related to food intake during a critical period (Beddington et al. 1976). In some salmon situations, the longer term reproductive response of predators can be ignored if we only consider pink (*O. gorbuscha*) and chum (*O. keta*) fry as prey, since they pass through the freshwater predation stage over a short time period relative to the resident predators' total time of food intake.

What is significant, then, to biologists concerned with manipulating juvenile salmon populations is the shape of the total response curve, the product of the numerical and functional responses. A Type III or "modified" Type II total response will have the same "threshold" characteristics as discussed above.

During early investigations of predation, it was initially thought that only predators that could learn would show Type III functional responses but it has been subsequently demonstrated that sigmoid responses may be more pervasive among predators (Hassell et al. 1977). The main classes of predators of juvenile salmon, fish and birds, show a variety of response types but most often Type III when more than one type of prey is available (reviewed by Murdoch and Oaten 1975).

Finally, the stability characteristics of a salmon population are critically dependent upon the shape of the total predator response curve (Peterman 1977). If the curve is a Type III or "modified" Type II relation, then a recruitment curve results that causes the salmon population to behave in a unique way. The population has "normal" behavior when at moderate or large sizes, but if for some reason, such as overexploitation, the population is reduced to a small size, the population will remain small even after the removal of the pressure that caused the initial decrease. Such "multiple-equilibria" or "multiple-domains-of-stability" phenomena have been commonly observed in fisheries (Holling 1973; Peterman 1977), and the existence of this "trap" at small population sizes can put serious constraints on management decisions. For example, a population that approaches the point of maximum sustainable yield is close to the boundary between the resident domain and the "trap" at low population sizes. Also, a population that is already in this "trap" needs to be enhanced by a certain amount to cross the boundary out of that domain; all smaller amounts of enhancement will be futile. Murdoch and Oaten (1975) review the literature dealing with the effect of functional response types on system stability properties. However their work along with others is misleading because it does not emphasize the effect of the total response.

When one considers the magnitude of predation mortality on salmon (first three figures), the significance of the process for salmon population dynamics, the apparent success of predator control programs (Foerster and Ricker 1941), and the extensive predation literature in other areas of ecology, it is astounding how little research has been done on the predation process in salmon. In particular, there is, with one exception (Ginetz 1970), virtually no publication to our knowledge that attempts to determine the forms of the basic components of predation on juvenile salmon.

In this paper we reexamine the relevant published

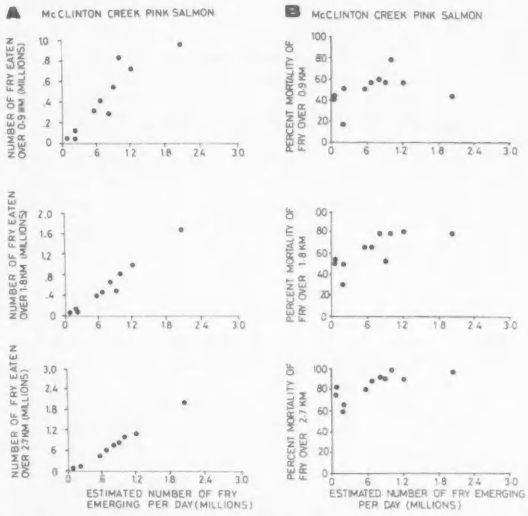
A McCLINTON CREEK PINK SALMON
B McCLINTON CREEK PINK SALMON
NUMBER OF FRY EATEN OVER 0.9 KM (MILLIONS)
PERCENT MORTALITY OF FRY OVER 0.9 KM
NUMBER OF FRY EATEN OVER 1.8 KM (MILLIONS)
PERCENT MORTALITY OF FRY OVER 1.8 KM
NUMBER OF FRY EATEN OVER 2.7 KM (MILLIONS)
PERCENT MORTALITY OF FRY OVER 2.7 KM
ESTIMATED NUMBER OF FRY EMERGING PER DAY (MILLIONS)
ESTIMATED NUMBER OF FRY EMERGING PER DAY (MILLIONS)

FIG. 5. A, Number of pink salmon fry eaten in relation to the minimum estimate of daily pink fry emergence for McClinton Creek, B.C. (calculated from data of Cameron 1958). Graphs show mortalities for each of three different distances of fry migration. B, Same data replotted as percent mortalities.

literature on the subject in order to sort out the predation components, but we restrict our comments in the present document to the functional response. The numerical response will be dealt with in a later paper. In addition, we derive a method for using existing daily counts of surviving fry, predators, and other information to estimate functional responses.

REEXAMINING THE DATA

We can attempt to remove the effect of changing predator numbers by looking at shorter time scale information than the data covering several years shown in Fig. 1–3. In addition, the phenomena, such as handling time, digestion rates, and gut capacity, that give rise to particular shapes of functional responses are more relevant on short time scales. Only three field experiments have been carried out on a short enough time scale to permit estimation of daily or weekly functional responses. In all cases, downstream-migrating fry were marked and released at different distances upstream from a counting fence. Predators were present in these stream sections. Total fry populations were enumerated daily at the fence and the survival rate of marked fry could be applied to the total fry counted at the fence to back-calculate the number of fry that emerged each night. In this way functional responses for the total predator complex could be estimated. As in the original studies, we assumed that all fry losses were due to predation; most fry killed from other causes would still be carried downstream to the counting weir. Note that data from these experiments could be biased due to increased vulnerability of marked fry. Cameron (1958) found significantly higher predation mortality on marked fish, while Foerster (1968, p. 156) claims there was no difference in mortalities between Cameron's thread-marking method and fin-clipping. In any case, the shape of the percent mortality curves would not be affected; only the absolute value of the mortality rates would be biased upward.

In Fig. 5A, the data of Cameron (1958), which cover a period of several months, indicate that the range of observed pink fry abundances probably only spanned the ascending limb of the functional response curve (cf. Fig. 4A). By using the more sensitive plot of percent mortalities (Fig. 5B), there was apparently a Type III or modified Type II response with a very small refugium (cf. Fig. 4B). Cameron gives no clear indication of changes in predator abundance during the time when these observations were made. In any case, at the highest prey counts seen, the percent mortality curves appeared to be peaking and were therefore close to the point where swamping would take effect and percent mortalities would decrease.

Data from another field experiment (of J. MacDonald reported in Foerster 1968) permit calculation of the response for the total predator complex that feeds on sockeye fry in Scully Creek, on Lakelse Lake, B.C. Figure 6 shows that for 1950 and 1952 at least, the predators (coho salmon yearlings, cutthroat trout, char, and sculpins) were operating at the very low end or linear portion of their functional responses; the prey abundances were not large enough to create any swamping effect. The curvilinear shape of the 1951 data in Fig. 6B suggests a Type III or "modified" Type II response, with predators operating mostly on the ascending limb of the percent mortality curve. Predator counts for Scully Creek show no drastic difference in species composition between 1951 and the other years, but variations in counts of predator populations within any year were not discussed.

In Hunter's (1959) Hooknose Creek study, fry counts were only published on a weekly basis for the fry-marking experiment, and his data also suggest that the predators in 1951 (coho yearlings and sculpins) were not being saturated (Fig. 7). Later in this paper, when Hunter's daily predator counts are included, we find that while predator numbers change considerably during each year due to emigration, the per-predator functional response is still near-linear.

Finally, the one study that explicitly set out to measure the functional response of rainbow trout (*Salmo gairdneri*) on sockeye (*O. nerka*) fry (Ginetz 1970) is difficult to interpret because of experimental design problems; individual predators were given larger numbers of prey on successive days. Therefore it is not possible to tell if the change in number eaten as prey density changed was due to the altered density or due to learning and experience by the predators. Given that caution, Ginetz's data suggest a Type II functional response.

In summary, existing data suggest that predators on juvenile salmon are not in general being swamped by any but the very largest prey populations. However, in most cases there is insufficient information on rapid, within-

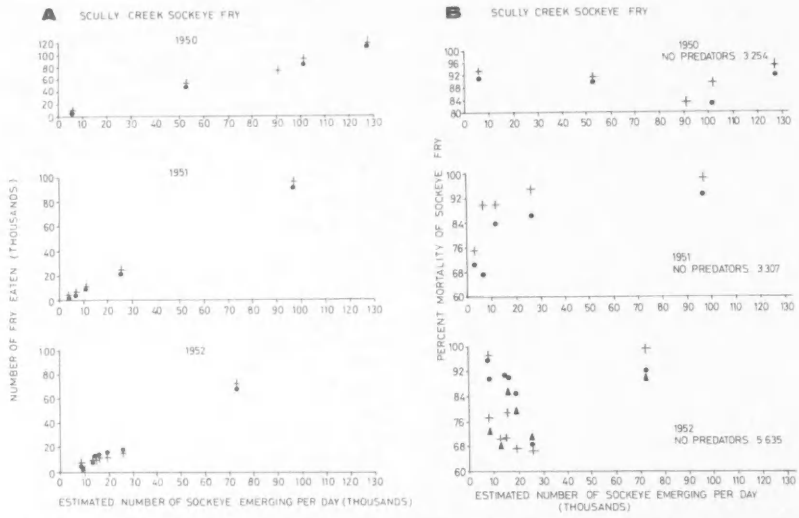

FIG. 6. A, Number of sockeye salmon fry eaten for each of 3 yr in relation to estimated daily fry emergence on Scully Creek, B.C. (calculated from data of J. MacDonald reported in Foerster 1968). Different symbols indicate mortalities over different distances of fry migration; ▲ for 152 m (500 ft), ● for 610 m (2000 ft), and + for 1219 m (4000 ft). B, Same data replotted as percent mortalities.

season changes in predator abundance and so functional responses cannot be completely sorted out.

Because of this lack of data on functional responses and because of the significance of such data for salmon management, we derived a method for using detailed field counts to estimate functional responses, and we applied the method to Hooknose Creek data.

Methods

The procedure we use is conceptually quite simple. If the daily number of fry that survive downstream migration is known along with the daily fry emergence, then the mortality is easily calculated by subtraction (assuming that most fry migrate downstream the same day they emerge from the gravel). This can be done for data throughout the fry emergence period to get a wide range of emerging fry abundances. There are numerous sets of daily counts at a weir for surviving fry of different species or different rivers, but there are no simultaneous enumerations of fry emergences, simply because of the logistical difficulties involved. Therefore, we had to devise some way of estimating the daily emergence pattern over time. This was done by assuming a fixed time delay between the appearance of the spawners at the counting weir the previous fall and emergence of their fry, as suggested by Hunter's (1959) analysis. As described later, our results were not very sensitive to alterations in the value of this delay time. This way of estimating emergence turned out to be the best available, since we could detect no relation in the data we used between timing of fry emergence and physical measurements such as cumulative temperatures, water flows, or cloud cover.

Dr J. G. Hunter very kindly provided us with his extensive set of data on the pink and chum salmon of Hooknose Creek, some of which were previously reported in Hunter (1959). His detailed analysis of the Hooknose Creek situation provided nine seasons of daily counts of fry surviving migration to the counting weir at the stream mouth, daily predator counts, daily upstream spawner enumerations, and samples of female egg contents. We refer the readers to Hunter's paper for further details of the situation. Since Hunter's (1959) predator data are shown in terms of the number of coho or sculpins leaving the stream area, we subtracted the daily count from the total predators for the season to determine the number of predators in the stream on any day. This method assumes that no predators are resident in the stream year-round and that predation loss due to nonfish sources is insignificant. These assumptions are supported by Hunter's (1959) data. Also,

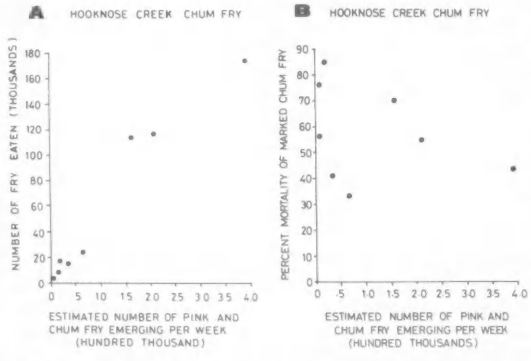

FIG. 7. A, Number of chum salmon fry eaten in relation to estimated pink and chum salmon fry emergence per week on Hooknose Creek, B.C. (after Hunter 1959). B, Same data replotted as percent mortalities.

Hunter (unpublished data) indicates that most of the predators stayed in the lower 500 m of the 2.9 km-long Hooknose Creek, which means that there was minimal effect of the depredations of large upstream predator populations on the number of fry available for predators farther downstream. Based on stomach-content analysis, Hunter (1959) determined that coho consumed at a given time about 1.33 times as many fry as the other major predators, prickly sculpins (*C. asper*). On this basis, he combined his estimate of predator populations into "predation units." Given the lack of separate, relevant evidence on coho and sculpin predation characteristics, we have only used Hunter's "predation unit" figures in our present analyses.

Model-Estimation Procedures

A simple model was built to permit estimation of daily fry emergence and consumption per predator. The model's assumptions are as follows:

1. Pink and chum salmon spawn immediately or with a fixed delay after reaching spawning areas and the number of deposited eggs is related to the number of incoming spawners through a fixed fecundity given by the average egg content per female in that year divided by 2 to take into account the male–female ratio, assumed equal to 1. In other words

$$D_p(t) = f_p S_p(t - d_p), \tag{1}$$

$$D_c(t) = f_c S_c(t - d_c), \tag{2}$$

where

$D_p(t)$, $D_c(t)$ = number of pink and chum eggs deposited in day t;

$S_p(t)$, $S_c(t)$ = number of incoming pink and chum spawners in day t during the fall;

f_p, f_c = fecundities;

d_p, d_c = delays.

2. The eggs have a fixed survival through the winter season and a fixed incubation time. Both parameters are assumed to be different in different years, but independent of the date of egg deposition in the same year. Therefore

$$E_p(t) = \gamma_p D_p(t - i_p), \tag{3}$$

$$E_c(t) = \gamma_c D_c(t - i_c), \tag{4}$$

where

$E_p(t)$, $E_c(t)$ = number of emerging pink and chum fry in day t;

γ_p, γ_c = egg-to-emerging fry survival coefficients;

i_p, i_c = incubation times.

3. The different predators can be lumped into predation units (see above) and hence are assumed to have the same functional response. Moreover pink and chum fry are assumed to be equally palatable and vulnerable, so that predators are sensitive only to the total number of emerged fry.

These assumptions are admittedly simple, but without data to the contrary, they had to be made for any estimation procedure to be applied. Changing most of these assumptions would not alter our findings concerning the qualitative form of the functional response, although absolute values of some parameters would differ.

Linear Predation Model

Since much of the data discussed above shows predators operating in the low, linear portion of their functional response curves, it seemed reasonable to begin by assuming a simple linear functional response with no satiation limit or depensation; the number of fry killed per predator is simply proportional to the number of emerged fry. Therefore

$$F(t) = E(t) - \alpha P(t) E(t), \tag{5}$$

where

$E(t) = E_p(t) + E_c(t)$,
= total number of emerging fry in day t;

$F(t)$ = number of fry counted at the weir in day t;

$P(t)$ = number of predation units present in the stream in day t;

α = predation mortality coefficient (proportion of emerging fry eaten per predator unit per day).

Substituting equations (1), (2), (3), and (4) into equation (5) and making the further assumption that $\gamma_p = \gamma_c = \gamma$, we finally get

$$F(t) = \gamma[f_p S_p(t - \tau_p) + f_c S_c(t - \tau_c)] - \alpha\gamma P(t)[f_p S_p(t - \tau_p) + f_c S_c(t - \tau_c)], \tag{6}$$

where

$$\tau_p = i_p + d_p, \quad \tau_c = i_c + d_c.$$

Now, define the new parameter $\delta = \alpha\gamma$ and suppose for the moment that τ_p and τ_c are fixed, so that $f_p S_p(t - \tau_p) + f_c S_c(t - \tau_c)$ is a known function, call it $S(t)$. Then equation (6) becomes

$$F(t) = \gamma S(t) - \delta P(t) S(t). \tag{7}$$

Of course a random factor must be introduced into equation (7) to take into account model errors, measurement errors, and fluctuations in survivals and incubation times. There are two main possibilities: either a multiplicative lognormal noise or an additive normal noise. The former assumption has consistently led to unrealistic estimates, such as negative survival rates, while the latter has given better results. Therefore, equation (7) has been modified as follows

$$F(t) = \gamma S(t) - \delta P(t) S(t) + n(t), \tag{8}$$

where $n(t)$ is an independent Gaussian noise with zero mean and variance σ^2.

Equation (8) can be considered for $t = 1, \ldots N$, N being the number of days each year during which data are available. Thus the problem of estimating γ and δ turns out to be a simple problem of linear regression, i.e. γ and δ can be estimated by minimizing the function

$$W = \sum_{t=1}^{N} [F(t) - \gamma S(t) + \delta P(t) S(t)]^2. \tag{9}$$

From now on, an estimate of any quantity x will be indicated by $\hat{x}$. After doing the regression we estimate the coefficient of mortality due to predation by

$$\hat{\alpha} = \frac{\hat{\delta}}{\hat{\gamma}}. \tag{13}$$

Thus, each year we obtain a new estimate of the slope of the relation between the number of prey eaten per predator per day and the number of prey available during that time.

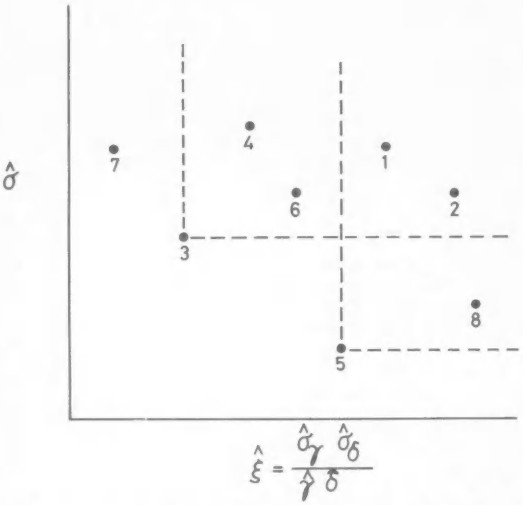

FIG. 8. Scheme for eliminating "dominated" solutions derived from the parameter estimation procedure.

Interested readers should refer to the Appendix; it describes the way variances are estimated and the regression method used, which utilizes daily counts of predators and daily estimates of emerging fry. The regression procedure is applied while keeping τ_p and τ_c (time delay between spawning and fry emergence) fixed. Since τ_p and τ_c vary from year to year and are known only approximately (~200 d from Hunter 1959), it is necessary to repeat this procedure for several possible combinations of τ_p and τ_c and set up criteria to discriminate among different combinations. The first obvious criterion is to eliminate those combinations that lead to negative values of γ and δ or to γ values $>100\%$.

As for the remaining combinations, it seemed reasonable to take into consideration the fit to the data and the reliability of the estimates $\hat{\gamma}$ and $\hat{\delta}$.

An indicator of the fit to data is obviously $\hat{\sigma}$, while an indicator of the reliability or stability of the estimates of $\hat{\gamma}$ and $\hat{\delta}$ is

$$\hat{\xi} = \frac{\hat{\sigma}_\gamma \hat{\sigma}_\delta}{\hat{\gamma}\hat{\delta}},$$

$\hat{\sigma}_\gamma$ and $\hat{\sigma}_\delta$ being the estimated standard deviations of $\hat{\gamma}$ and $\hat{\delta}$.

Thus each combination of τ_p and τ_c is associated with a pair, $\hat{\sigma}$ and $\hat{\xi}$. A natural discrimination procedure is to eliminate all the dominated combinations, i.e. those combinations such that there is another combination with smaller $\hat{\sigma}$ and smaller $\hat{\xi}$ (e.g. Fig. 8, where combinations 1, 2, 4, 6 are dominated by 3; 8 is dominated by 5, but not by 3 or 7; 3, 5, 7 are not dominated). Finally all the nondominated solutions (in general, there are many) are taken into account because they are considered equally good.

SATURATING PREDATION MODEL

The above linear predation model, which assumes that the number eaten per predator is strictly proportional to the number of prey available, did not give reasonable solutions for 2 out of the 9 yr of data. In particular, the optimal combinations of parameter values, in terms of the criteria described above, turned out to be on the boundary with combinations that had to be eliminated because the corresponding estimate $\hat{\gamma}$ was $>100\%$. However, this fact is not surprising, since in the 2 yr in question, 1953 and 1954, the number of fry counted at the weir, and hence the number of emerged fry, was unusually high; 1.2 million as opposed to 1–500 000 in most other years. Therefore, it may not be realistic to use, for these 2 yr at least, a predator functional response where no satiation occurs. We introduce a saturating predation model of the form described by Holling (1959b):

$$F(t) = \gamma S(t) - \frac{\alpha P(t)\gamma S(t)}{1 + \beta\gamma S(t)}, \tag{16}$$

where the symbols are as in the linear model, and β = a measure of handling time and attack rate. Let $\delta = \alpha\gamma$ and $\epsilon = \beta\gamma$, then substituting these into equation (16) we have

$$F(t) = \gamma S(t) - \frac{\delta P(t)S(t)}{1 + \epsilon S(t)}. \tag{17}$$

We want to find the combination of γ, δ, and ϵ that minimizes the function

$$W = \sum_{t=1}^{N} \left(F(t) - \gamma S(t) + \frac{\delta P(t)S(t)}{1 + \epsilon S(t)} \right)^2. \tag{18}$$

If we fix ϵ, we get the same type of problem as described above, and γ and δ can be directly estimated by regression. We then search for the best ϵ in a given range.

Results

Table 1 presents the results obtained with the linear predation model assumption. Only the nondominated solutions are reported, as defined by the criteria described above. Note that in several years there is more than one combination of τ_p and τ_c, the incubation times and egg-laying delays in days, which give a solution. Notice further that $\hat{\alpha}$, the estimated slope of the relation between number of prey available each day and number eaten per predator per day, is fairly stable from year to year. In fact, these estimated values are close to the value obtained in the one experiment done by Hunter (1959). If his data for the 1951 experiment are replotted as number eaten per predator unit per week as a function of number of emerging fry per week, then the slope of the apparently linear relation is about 1.3×10^{-4}, or slightly greater than the value estimated by our scheme for 1951 (Table 1).

However, when more than one τ_p and τ_c combination is present in the same year, $\hat{\gamma}$ and $\hat{\delta}$ are highly variable and show a positive correlation. The estimated correlation coefficient $\hat{p}$ between $\hat{\gamma}$ and $\hat{\delta}$ (which can be easily derived from $\hat{V}_*$ — see Appendix) is always very high, >0.993. This implies that a confidence region for $\hat{\gamma}$ and $\hat{\delta}$ is shaped like that in Fig. 9A, thus pointing out great uncertainty in the estimation of γ and δ, and consequently α.

This situation is due to insufficient variation in the number of predators within each fry migration season. In most years very few predators leave the stream until most fry have emerged and migrated downstream (Hunter 1959). Thus, we run into the classical ecological problem of the natural system not being perturbed enough to provide data over a wide range of values to permit estimation of functional relations.

TABLE 1. Results of applying the functional response parameter estimation scheme to the Hooknose Creek data. Symbols are defined in text, and only the nondominated solutions are shown.

Year	τ_p	τ_c	$\hat{\gamma}\%$	$\hat{\delta}\cdot 10^5$	$\hat{\alpha}\cdot 10^4$	$\hat{\sigma}_\gamma\%$	$\hat{\sigma}_\delta\cdot 10^5$
1948	211	193	15.9	1.24	0.78	1.64	0.13
1949	217	197	42.0	6.96	1.66	4.80	0.89
	217	204	25.7	3.99	1.55	3.45	0.67
	217	206	17.4	2.29	1.32	2.75	0.54
1950	213	202	37.7	7.12	1.89	3.11	0.64
1951	210	212	65.2	7.50	1.15	27.70	3.64
	216	212	45.1	4.52	1.00	18.20	2.41
1952	201	205	87.2	10.90	1.26	15.00	2.18
	201	206	78.1	9.59	1.23	14.20	2.07
	201	207	72.0	8.64	1.20	13.10	1.92
	206	204	75.8	9.29	1.23	14.10	2.08
	208	205	62.9	7.28	1.16	11.50	1.71
	209	206	47.6	5.00	1.05	10.90	1.63
1955	203	192	59.1	5.05	0.85	14.50	1.27
	205	192	51.6	4.40	0.85	13.80	1.21
	206	192	46.0	3.91	0.85	13.20	1.16
	208	191	39.4	3.34	0.85	12.80	1.14
	208	192	41.0	3.49	0.85	13.30	1.18
1956	213	214	25.3	3.30	1.30	2.42	0.35

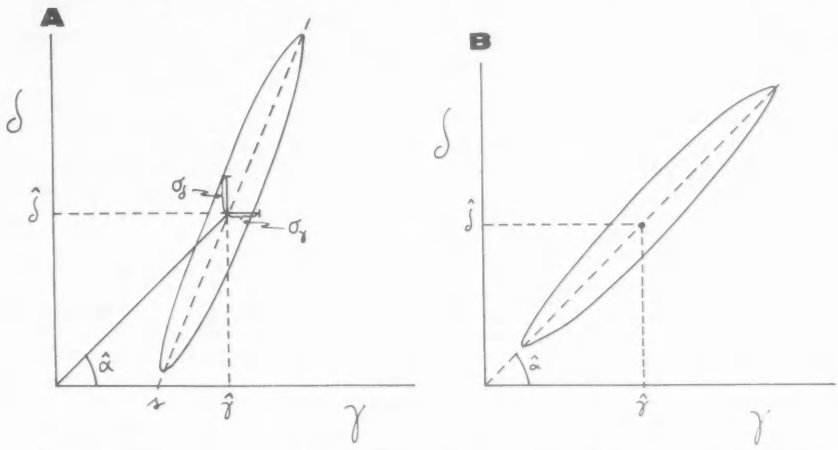

FIG. 9. A, Situation suggested by data in Table 1. Estimates of γ and δ are highly correlated, even though they are both quite variable. Thus, the estimate of α could also be quite variable. B, Results in Table 2 show that, in fact, α can be measured quite precisely because s is very close to zero. Thus Fig. 9A is not correct and the true representation of the situation is as shown here.

Notice that in the limiting case of constant number of predators [$P(t) = \bar{P}$ for all t] it would only be logically possible to estimate an overall egg-to-migrant fry survival, s, where

$$s = \gamma(1 - \alpha\bar{P}) \tag{19}$$

because there would be infinite combinations of γ and α that give rise to the same s. In other terms $\hat{p}$ would equal 1 and $\hat{\gamma}$ and $\hat{\delta}$ would be linearly related so that only the intercept s in Fig. 9A could be estimated.

However, there is a more direct way to determine if the estimates of α are as critically dependent on $\hat{\gamma}$ and $\hat{\delta}$ as suggested above; using terms defined in the Appendix, the variance of $\hat{\alpha}$ can be directly estimated as

$$\hat{\sigma}_z^2 = \lambda^T \hat{V}_\pi \lambda = \frac{1}{\hat{\gamma}^2}(\hat{\alpha}^2\hat{\sigma}_\gamma^2 - 2\hat{\rho}\hat{\sigma}_\gamma\hat{\sigma}_\delta\hat{\alpha} + \hat{\sigma}_\delta^2), \tag{20}$$

where

$$\lambda^T = \left(\frac{\partial z}{\partial \gamma}\frac{\partial z}{\partial \delta}\right).$$

TABLE 2. The standard deviation of the α values of Table 1 for the different combinations of τ_p and τ_c.

Year	τ_p	τ_c	$\hat{\sigma}_\alpha \cdot 10^6$
1948	211	193	0.41
1949	217	197	2.85
	217	204	5.62
	217	206	10.60
1950	213	202	1.91
1951	210	212	7.35
	216	212	13.20
1952	201	205	3.78
	201	206	4.55
	201	207	5.29
	206	204	4.95
	208	205	6.26
	209	206	10.50
1955	203	192	0.63
	205	192	0.71
	206	192	0.82
	208	191	1.31
	208	192	1.20
1956	213	214	1.92

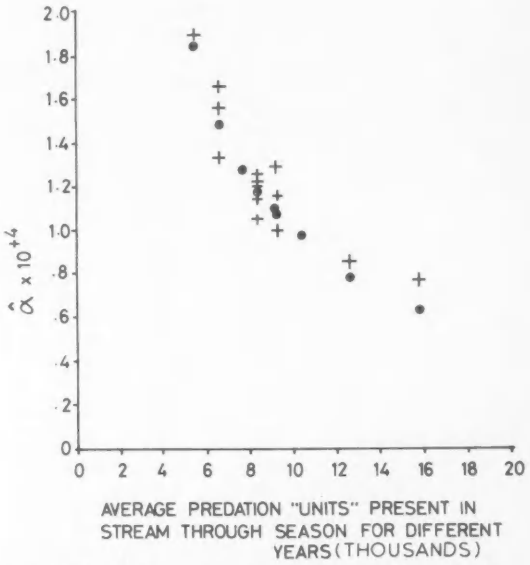

FIG. 10. The relation between $\hat{\alpha}$, the predation coefficient, and the number of predation "units" in Hooknose Creek in each year; ● points are calculated from Hunter's (1959) data by assuming that $\hat{\alpha} = 1/\bar{P}$ (see text); + points are the values of $\hat{\alpha}$ shown in Table 1 and calculated from the more complex, linear estimation procedure.

The results shown in Table 2 indicate that α can be estimated fairly precisely. This apparent contradiction with the conclusion of the paragraph above can be explained by pointing out that the situation, rather than being like that in Fig. 9A, is actually like that in Fig. 9B, so that α can be estimated quite well, even if the estimate of γ is very poor.

When the estimates, α, of the slope of the functional response in different years are plotted as a function of the number of predation units present in those years, there is an inverse relation (Fig. 10). Thus, there is some form of competition among the predators; for any given prey density, fewer prey are eaten per predator when predator numbers are large than when they are small.

This competition effect is also predicted from equation (19), if predator numbers are assumed constant throughout a given season and if the overall egg-to-migrant fry survival is very small and close to zero. In such a limiting case, where both assumptions are valid, as discussed above, and where γ, the egg-to-emerging fry survival is greater than zero, equation (19) reduces to $\alpha = 1/\bar{P}$. When α is estimated in this way by using for $\bar{P}$ Hunter's data on the average number of predator units throughout the season, the values come out remarkably close to the $\hat{\alpha}$ estimates of Table 1 (Fig. 10).

Finally, as discussed in the Methods there were 2 yr, 1953 and 1954, for which the linear predation model gave unacceptable results, and the data for these years are not reported in Tables 1 of 2. We applied the saturating predation model to 1953 and 1954 but found that $\hat{\gamma}$, the egg-to-emerging fry survival rate, was always negative, as was $\hat{\delta}$; $\hat{\gamma}$ was still negative even when $\hat{\delta}$ was fixed at a value of 1.2×10^{-4}. These unrealistic results suggest that some more complicated process than either a linear or a saturating predation model must have been operating in those years, or that the information contained in 1953 and 1954 data are not sufficient for parameter estimation.

Discussion

Stable, consistent results were obtained for the parameters of the linear predation model, and the results were very close to the independent experimental measurement of the parameter. However, most predators have to have some saturating feeding function; gut capacity and handling time must limit the amount of food eaten even if there is a large food supply available (Holling 1959a; Murdoch and Oaten 1975). Therefore, our data analysis for the Hooknose Creek situation implies that the predators were operating down at the low, linear end of their functional response curves in most years, below the prey levels where satiation would show an effect. This conclusion is similar to that drawn in Ricker (1941) and in our introduction concerning some other studies of predation on salmon fry. While some of the data we reviewed demonstrated near-satiation at the highest prey numbers enumerated, most did not.

Thus, the need for experimental measurement of functional responses of predators on juvenile salmon is reemphasized. We cannot hope that the natural system fluctuations will be wide enough to tell us above what fry

density percent predation mortality will drop off significantly. Yet if these predators have Type III or modified Type II responses, many salmon enhancement projects may only increase the proportion of salmon fed to predators instead of increasing the proportion caught by fishermen. If predation studies cannot be done before enhancement, then experimental measurement of functional responses should be combined with enhancement programs to take advantage of the perturbations in fry abundances.

Our results also indicate that the slope, α, of the functional response relation decreases with increasing number of predators. This could be occurring because of lower encounter rates caused in turn by smaller predator territories in the presence of large predator numbers. In any case, this observed competition effect brings up the possibility that predator control programs may actually increase the efficiency of individual predators by decreasing the competition among the remaining members of the population. For any particular situation, the significance of this effect can only be established if we know how the functional response curves of the predators vary with predator density. Again, further experimental studies are called for.

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Appendix

The parameter estimation procedure for the model parameters discussed in the text are as follows. We introduce the following matrices and vectors

$$\mathbf{J} = \begin{pmatrix} S(1) & -P(1)S(1) \\ S(2) & -P(2)S(2) \\ \cdot & \cdot \\ \cdot & \cdot \\ \cdot & \cdot \\ S(N) & -P(N)S(N) \end{pmatrix}, \quad \hat{\boldsymbol{\pi}} = \begin{pmatrix} \hat{\gamma} \\ \hat{\delta} \end{pmatrix}, \quad \mathbf{Y} = \begin{pmatrix} F(1) \\ F(2) \\ \cdot \\ \cdot \\ \cdot \\ F(N) \end{pmatrix}.$$

It is well known (Kendall and Stuart 1962) that the solution of the linear regression problem is given by

$$\hat{\boldsymbol{\pi}} = (\mathbf{J}^T\mathbf{J})^{-1}\mathbf{J}^T\mathbf{Y}. \tag{10}$$

Kendall and Stuart (1962) also show that estimates $\hat{\sigma}^2$ of the noise variance and $\hat{V}_\pi$ of the parameter covariance matrix can be obtained via the formulas

$$\hat{\sigma}^2 = \frac{\sum_{t=1}^{N} [F(t) - \hat{\gamma}S(t) + \hat{\delta}P(t)S(t)]^2}{N - 2}, \tag{11}$$

$$\hat{V}_\pi = \hat{\sigma}^2(\mathbf{J}^T\mathbf{J})^{-1}. \tag{12}$$

Actually, equation (10) has not been used directly to get $\hat{\pi}$. Instead, $\hat{\pi}$ has been computed by a recursive least squares method. This method consists of computing recursively estimates $\hat{\pi}_K$ that are based on K data. In other words, $\hat{\pi}_K$ is the parameter vector that minimizes the function

$$W_K = \sum_{t=1}^{K} [F(t) - \gamma S(t) + \delta P(t)S(t)]^2.$$

What is important in this method (for details see Eykhoff 1974) is the possibility of obtaining $\hat{\pi}_{K+1}$ from $\hat{\pi}_K$ by means of simple recursion formulas and thus finally getting $\hat{\pi}$, since $\hat{\pi}_N$ is obviously equal to $\hat{\pi}$. Some matrix notations are necessary to introduce these formulas. Let

$$\mathbf{J}_{K+1} = \begin{pmatrix} S(1) & -P(1)S(1) \\ S(2) & -P(2)S(2) \\ \cdot & \cdot \\ \cdot & \cdot \\ \cdot & \cdot \\ S(K) & -P(K)S(K) \\ S(K+1) & -P(K+1)S(K+1) \end{pmatrix} = \begin{pmatrix} \mathbf{J}_K \\ r_{K+1}^T \end{pmatrix},$$

$$\mathbf{X}_{K+1} = (\mathbf{J}_{K+1}^T \mathbf{J}_{K+1})^{-1}.$$

Then, it is possible to prove that the following recursive formulas hold (Eykhoff 1974):

$$\hat{\pi}_{K+1} = \hat{\pi}_K + \frac{\mathbf{X}_K r_{K+1}[F(K+1) - r_{K+1}^T \hat{\pi}_K]}{1 + r_{K+1}^T \mathbf{X}_K r_{K+1}}, \tag{14}$$

$$\mathbf{X}_{K+1} = \mathbf{X}_K - \frac{\mathbf{X}_K r_{K+1} r_{K+1}^T \mathbf{X}_K}{1 + r_{K+1}^T \mathbf{X}_K r_{K+1}}. \tag{15}$$

Note that by equations (14) and (15) it is possible to obtain π_{K+1} and $\mathbf{X}_{K+1}$ from π_K and $\mathbf{X}_K$ without any matrix inversion. Moreover, observe that $\mathbf{X}_N = (\mathbf{J}^T\mathbf{J})^{-1}$, which is useful to compute the estimate of the covariance matrix $\hat{V}_\pi$.

Of course the algorithm given by equations (14) and (15) must be initialized. This can be done simply by computing directly

$$\mathbf{X}_2 = (\mathbf{J}_2^T \mathbf{J}_2)^{-1}$$

and

$$\hat{\pi}_2 = \mathbf{X}_2 \mathbf{J}^T{}_2 \mathbf{Y}_2, \quad \mathbf{Y}_2 = \begin{pmatrix} F(1) \\ F(2) \end{pmatrix}.$$

The advantages of the recursive least squares method are

1. It is numerically quite safe because it avoids the direct inversion of $\mathbf{J}^T\mathbf{J}$, which can be a very ill-conditioned matrix, with elements that are very large numbers.

2. It is possible to monitor how the estimates of γ and δ vary when adding more and more data. It would be of course desirable to obtain "stabilized" estimates, i.e. that do not vary too much when using the final part of the data.

Acidic Precipitation in South-Central Ontario: Recent Observations

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DILLON, P. J., D. S. JEFFRIES, W. SNYDER, R. REID, N. D. YAN, D. EVANS, J. MOSS, AND W. A. SCHEIDER. Acidic precipitation in south-central Ontario: recent observations. J. Fish. Res. Board Can. 35: 809–815.

Precipitation in south-central Ontario, with mean pH between 3.95 and 4.38 and frequent event pH's of <4.0, is more acidic than that in the Sudbury, Ontario, region and in Scandinavia, and as acidic as that in the northeastern USA. As in New England, a major component of the total acidity is strong mineral acid. Because most lakes in south-central Ontario have very low buffering capacities (10–200 $\mu eq \cdot L^{-1}$), high acid loadings are likely to lead to acidification of many lakes and streams in the forseeable future. Although it is not yet possible to estimate the time required for this to happen, there is already some evidence of declining buffering capacity in a few lakes.

Key words: acidic rain, buffering capacity, acidic lakes, precipitation, alkalinity

DILLON, P. J., D. S. JEFFRIES, W. SNYDER, R. REID, N. D. YAN, D. EVANS, J. MOSS, AND W. A. SCHEIDER. Acidic precipitation in south-central Ontario: recent observations. J. Fish. Res. Board Can. 35: 809–815.

La précipitation dans le centre-sud de l'Ontario, avec pH moyen situé en 3.95 et 4.38 et des pH inférieurs à 4.0 étant d'occurrence commune, est plus acide que celle de la région de Sudbury de l'Ontario et de la Scandinavie, et est aussi acide que celle du nord-est des États-Unis. Comme en Nouvelle-Angleterre, un acide minéral fort est une composante majeure de l'acidité totale. Etant donné que la plupart des lacs du centre-sud de l'Ontario ont un pouvoir tampon très bas (10–200 $\mu éq \cdot L^{-1}$), de fortes charges acides sont de nature à entraîner l'acidification de plusieurs lacs et cours d'eau dans un avenir prévisible. Bien qu'on ne soit pas encore en mesure d'estimer le temps requis pour que ce phénomène se produise, on a déjà des preuves d'un déclin du pouvoir tampon de quelques lacs.

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THE occurrence of acidic rain and the resultant acidification of freshwater lakes and rivers has been recognized as a widespread nonlocalized problem in Scandinavia (Odén 1968, 1976) and in the northeastern USA (Likens 1976; Schofield 1976). In Ontario, however, acidification has been documented only in the vicinity of Sudbury (Gorham and Gordon 1960; Conroy et al. 1974) and in the La Cloche Mountain lakes about 80 km to the southwest (Beamish and Harvey 1972; Beamish 1974). This is not surprising since Sudbury is the site of the world's largest single point source of sulphur dioxide (Summers and Whelpdale 1976), and the airborne conversion of sulphur dioxide to sulphuric acid is well documented (Brosset 1973). Furthermore, the La Cloche Mountains, a series of quartzite ridges that provide little or no buffering capacity, are located in line with one of the prevailing wind directions from Sudbury (Beamish 1976).

A survey of lakes within a 160-km radius of Sudbury has identified lakes with pH <5.5, a level often considered critical for reproductive success of some fish species (EIFAC 1969), as far as 130 km distant in a north–northeast direction and 60 km in a south–southwest direction (Conroy et al. 1975). However, many lakes within the immediate vicinity have not been acidified despite significant atmospheric inputs. Three major factors govern the pH of lakes in the Sudbury area: (a) the rate of input of strong acid; (b) the location of the lake relative to the prevailing winds, which modifies (a); and (c) the geochemistry of the surficial sediments and the bedrock, which determines the buffering capacity of the lake and the runoff waters entering it (Kramer 1975). The last factor can override all others; that is, local calcareous soil or rock deposits can assimilate hydrogen ions and continue to provide a buffer system for waters located there.

Other parts of Ontario are underlain by silicate bedrock of low solubility and little buffering capacity with only a shallow glacial till overburden, or none at all. Thus, the potential for acidification of lakes in other areas of Ontario exists. One such area is a major recreational region of the province, the Muskoka–Haliburton–Parry Sound–Nipissing region in south-central Ontario

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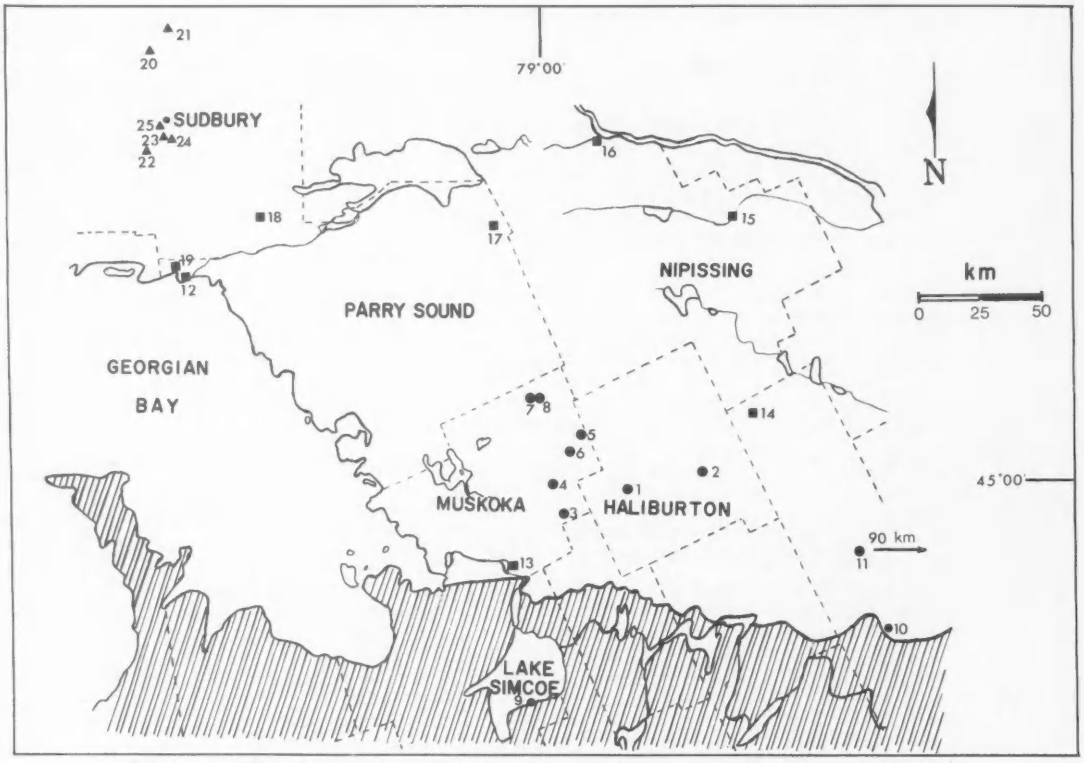

FIG. 1. Location of precipitation collection sites according to county. Shaded area is Paleozoic bedrock; clear area is Precambrian. Station numbers refer to Tables 1 and 2.

(Fig. 1). In this report we present evidence to suggest that acidic rain either already has or soon will cause a severe environmental problem in south-central Ontario.

Study Area

The portion of Ontario lying east of Georgian Bay, south of Lake Nipissing, and north of the Precambrian Shield–Paleozoic boundary is underlain almost entirely by Precambrian rock composed of granite, granite gneiss, granite pegmatite, and migmatite. Smaller areas of Precambrian sediments and volcanics exist, particularly to the southeast. The overburden of this area consists almost exclusively of a shallow till (<1 m) but the bedrock is commonly exposed. There are, however, localized areas of Precambrian spillways that follow ancient riverbeds, and small areas of sand plains, clay plains, and kame moraines. The Paleozoic region to the south consists principally of clastic and carbonate sediments of substantially higher buffering capacity. For a detailed discussion of the physiography of the region, see Chapman (1975).

The many lakes in this region are, as a result, dilute and weakly buffered. A survey between 1959 and 1962 of 310 lakes throughout Ontario (Ryder 1964) was used to draw isopleths of total alkalinity (Ryder's fig. 7) for the province. The lakes of the entire region of south-central Ontario were characterized as having $<25\ mg \cdot L^{-1}$ total alkalinity as $CaCO_3$ with a number of them between 6 and $10\ mg \cdot L^{-1}$. A subsequent survey (Sparling and Nalewajko 1970) of 70 lakes in southern Ontario again demonstrated that lakes in this region were frequently dilute and had total alkalinities of $<10\ mg\ CaCO_3 \cdot L^{-1}$, with one observation (Wren Lake) as low as 3.5.

Materials and Methods

Collection of Samples

Precipitation event samples ("wet" only) were collected with automatic battery-operated, moisture-activated samplers (Applied Earth Sciences Consultants design). Samples collected at or near the laboratory site (Dorset, Red Chalk Lake) were analyzed immediately after precipitation events, while those more distant (Fig. 1) were analyzed weekly or less often if no precipitation occurred in a given week. One event sampler (Dorset) was modified for winter use by installation of a thermostatically controlled electric light bulb in the sample compartment. Snow samples were rapidly melted and kept in the liquid state.

Bulk precipitation samples were collected with either 43-cm-diameter, 63-cm-high polyethylene containers (snow samples) or standard, 10-cm diameter, polycarbonate precipitation gauges with 200 μm Nitex mesh at the base (April–November) to prevent contamination by insects. Any visibly contaminated samples were discarded. Two bulk collectors

were installed at Harp Lake, one onshore and one on a raft.

Samples from lakes were collected weekly at 2-m intervals through the epilimnion of each lake and monthly through the entire water column in the winter with a Van Dorn bottle, weighted according to the volume of the stratum represented prior to chemical analyses, then recombined.

All glassware was washed with 2 M HCl, rinsed (at least 6 times) with deionized distilled water, then rinsed several times with the appropriate lake or stream water prior to sample collection. Great care was taken to exclude air bubbles from the samples.

Chemical Analyses

The pH of precipitation and lake samples was determined as soon after sampling as possible with a Corning Digital 109 pH meter, after appropriate buffer calibration. Sulphate was analyzed by the methyl thymol blue technique (Ontario Ministry of the Environment 1975).

The standard alkalinity determination employed by many laboratories involves titration of the samples to a pH of 4.5, i.e. to the assumed equivalence point of the bicarbonate protonation reaction. This assumption is reasonably good for high alkalinity samples (>4 meq$\cdot$L^{-1}) but tends to be an overestimate for low alkalinity samples, since the equivalence point occurs at pH >4.5. The correct equivalence pH can be determined by the Gran technique (summarized by Stumm and Morgan 1970). Extrapolation of a plot of $(V_o + V)$ $[H^+]$ vs. V to the V-axis intercept (where V_o = volume of sample (millilitres), V = volume of titrant added (millilitres), and $[H^+]$ = proton concentration = 10^{-pH}) for $[H^+]$ equivalence proton concentration yields the volume of titrant required to reach equivalence.

Since most of our routine samples were titrated to a fixed endpoint of pH = 4.5, these values are identified as "total fixed-endpoint alkalinities" in the following discussion, while the more meaningful alkalinities determined to the inflection point of the titration curve are termed "total inflection-point alkalinities."

Acidity and alkalinity titrations were performed by constant addition of standardized NaOH or H_2SO_4 at 0.1 to 0.4 mL$\cdot$min^{-1} to a continuously stirred 100.0-mL aliquot of sample. Titrant addition was achieved through use of a peristaltic pump, the addition rate having been previously calibrated. Progress of the titration was followed by constantly monitoring the pH of the solution with a meter producing a recorded output. The strip-chart recorder was calibrated by determining the pen position for various buffer solutions (pH = 4.00, 7.00, and 9.00). This calibration procedure was carried out after every three samples to ensure that meter drift was not a problem. All titrations were carried out under a continuously flushed atmosphere of inert gas (N_2 or He) in order to prevent the absorption of CO_2 during the acidity titration. The titrations were allowed to proceed to pH >9 for acidity determinations and pH <4 for alkalinity determinations. The acidity titrations were repeated with an aliquot that was bubbled with N_2 or He for at least 10 min prior to titration.

From the acidity titrations the following information was calculated: (a) total acidity, from the amount of NaOH required to raise the sample pH to 9.00; (b) carbonate acidity, from the difference between (a) and the acidity measured for a CO_2-degassed sample; (c) free acidity, from the initial pH; free acidity = 10^{-pH}; (d) "weak acid" acidity, from the difference between the total acidity and the sum of carbonate acidity and free acidity.

With this technique, titration of strong acid solutions will show a significant "weak acid" component due to the difference between the equivalence pH of the strong acid (i.e. 7.00) and the endpoint pH. Acidity values were thus corrected for this component which is most significant for samples of very low acidity (correction is $\simeq 15$ μeq$\cdot$L^{-1}).

From the alkalinity titrations, the following information was calculated: (a) total inflection-point alkalinity as the amount of standardized acid titrant required to lower the sample pH to the bicarbonate–carbonic acid equivalence point; (b) total fixed-endpoint alkalinity as the amount of acid titrant required to lower the sample pH to 4.5.

Results and Discussion

The chemistry of precipitation indicates that a potentially serious problem currently exists in south-central Ontario. This conclusion is supported by the low and possibly declining buffering capacities of some lakes.

Precipitation Chemistry

The pH and sulphate concentrations of precipitation event and bulk samples collected at 11 sites (Fig. 1) for varying time periods between May 1976 and April 1977 are summarized in Table 1. The first eight stations are located on the Precambrian Shield in four counties of south-central Ontario, while the last three are located either just off the Shield or on its boundary with areas of Paleozoic bedrock to the south and east.

The mean pH (mean volume-weighted hydrogen ion concentration in microequivalents per litre converted to its negative logarithm) of bulk samples varied between 4.06 and 4.22 (87–60 μeq$\cdot$L^{-1}) with an overall mean of 4.14 at the eight sampling locations on the Precambrian Shield. The range of means was 4.78–5.79 (17–2 μeq$\cdot$L^{-1}) with an overall mean of 5.31 at the three stations on the Shield periphery. Ranges of pH at individual stations also were quite different at the three off-Shield stations; all eight Shield stations had individual bulk samples with pH well under 4.0 (up to 460 μeq$\cdot$L^{-1}), while the remaining three had no bulk samples of pH <4.0 (minimum 4.12). For the Shield stations, a total of 24 bulk samples out of 86 (28%) had pH <4.0. These data support the suggestion of Winkler (1976); that is, precipitation samples collected in regions dominated by a carbonate terrain may be neutralized to some extent by entrained particulates. In the Precambrian regions of this study, the geological terrain is dominated by silicate rocks, and the smaller neutralizing capacity of this entrained material results in lower pH values in collected samples.

The mean pH of event samples at the six Shield stations with appropriate collectors varied from 3.95 to 4.38 (112–42 μeq$\cdot$L^{-1}). However, the Dorset station, with the only winterized event collector, had a low mean pH (3.95), reflecting several very low event pH's (minimum 2.97) measured in the winter of 1976–77. As described previously, all other event collectors were not operable under freezing conditions. Excluding the Dorset station, the range of means is reduced to 4.17–

TABLE 1. Differences in volume-weighted hydrogen ion (as pH and $\mu eq \cdot L^{-1}$) and $SO_4^=$ concentrations ($mg \cdot L^{-1}$ and $\mu eq \cdot L^{-1}$) between bulk and event precipitation samples at eight stations on the Precambrian Shield in south-central Ontario and three stations to the south and east. The mean pH was calculated as negative logarithm of the volume-weighted arithmetic mean H^+ concentration. The pH's in parentheses were calculated as the volume-weighted arithmetic mean pH. Numbers refer to Fig. 1.

				H^+			$SO_4^=$	
				pH				
Station	Fraction	Period of collection	*n*	Mean	Range	$\mu eq \cdot L^{-1}$	$mg \cdot L^{-1}$	$\mu eq \cdot L^{-1}$
1, Carnarvon	Bulk	Aug. 1976–May 1977	12	4.06 (4.16)	3.64–5.87	87	4.1	85
	Event	Sept. 1976–Oct. 1976	4	4.19 (4.19)	4.15–4.26	64	3.7	76
2, Eagle Lake	Bulk	Aug. 1976–May 1977	9	4.17 (4.27)	3.19–4.76	68	3.3	69
	Event	Aug. 1976–Sept. 1976 + May 1977	5	4.27 (4.28)	4.10–4.40	53	3.3	69
3, Vankoughnet	Bulk	July 1976–Mar. 1977	14	4.15 (4.20)	3.78–4.66	71	3.3	68
	Event	Apr. 1976–Sept. 1976	16	4.30 (4.60)	3.93–7.70	50	2.6	54
4, Gullfeather	Bulk	Aug. 1976–Mar. 1977	10	4.22 (4.45)	3.83–5.32	60	2.6	53
5, Dorset	Bulk	Nov. 1976–Apr. 1977	16	4.12 (4.27)	3.34–5.80	76	3.0	63
	Event	Nov. 1976–Apr. 1977	20	3.95 (4.42)	2.97–5.93	112	2.4	50
6, Red Chalk	Bulk	Aug. 1976–May 1977	9	4.14 (4.17)	3.80–4.40	73	2.7	57
	Event	July 1976–Sept. 1976	10	4.17 (4.24)	3.92–4.73	67	3.3	70
7, Harp Lake	Bulk	June 1976–Oct. 1976	6	4.17 (4.24)	3.69–4.36	68	1.5	31
	Event	June 1976–Oct. 1976	9	4.38 (4.45)	4.07–5.36	42	2.7	56
8, Harp Raft	Bulk	Aug. 1976–Mar. 1977	10	4.11 (4.15)	3.79–4.46	78	3.2	67
9, Sibbald Park	Bulk	July 1976–Sept. 1976	5	4.78 (4.82)	4.12–6.28	17	—	—
	Event	May 1976–Sept. 1976	13	4.42 (4.75)	3.93–6.89	38	3.5	72
10, Madoc	Bulk	Sept. 1976–Oct. 1976	2	5.79 (5.89)	5.50–6.21	2	—	—
	Event	May 1976–Oct. 1976	9	4.35 (4.78)	3.98–6.71	45	3.7	77
11, Silver Lake	Bulk	July 1976–Oct. 1976	8	5.35 (6.00)	4.84–6.70	5	2.5	52
	Event	July 1976–Sept. 1976	8	4.37 (4.63)	4.03–6.14	42	2.7	55

4.38 (68–42 $\mu eq \cdot L^{-1}$), with 15 of 63 (24%) event samples having pH <4.0. Mean event pH at the three off-Shield stations, however, varied between 4.35 and 4.42 (45–38 $\mu eq \cdot L^{-1}$). The mean pH's of event samples at the six Shield stations were therefore only slightly lower than those of the three off-Shield locations. These results indicate that on the Shield the mean pH of bulk samples was lower than that of the event samples, while for the three stations (Sibbald Park, Madoc, Silver Lake) not on the Shield the converse was true.

Others have investigated the acidic nature of precipitation in south-central Ontario. Nicholls and Cox (1977) measured the pH of 14 bulk samples in 1974 at Harp Lake; their mean pH of 3.96 is in close accord with our results. Table 2 summarizes bulk precipitation data collected by J. R. Kramer (unpublished data) in the period 1973–75 at seven locations (Stations 12–18) surrounding our study area and by Beamish and Van Loon (1977) at Lumsden Lake (Station 19) in Killarney Park in 1972–73. We have also included data collected at six locations (Stations 20–25) in the Sudbury region where we have employed bulk precipitation collectors. Our measured pH's in the Sudbury region are very close to those measured by Beamish 3–4 yr earlier at Lumsden Lake. The pH's of our eight bulk precipitation stations on the Precambrian Shield southeast of Sudbury (average pH of 4.14, or 72 $\mu eq \cdot L^{-1}$) were 50% higher in H^+ content than our Sudbury stations and almost identical to J. R. Kramer's (unpublished data) monthly bulk sample means measured 1–3 yr earlier in the surrounding area.

Studies by Likens et al. (1975) have demonstrated that precipitation falling at Hubbard Brook in the northeastern USA had a mean annual pH ranging from 4.03 to 4.21 between 1970 and 1974, almost identical to that in south-central Ontario. Dovland et al. (1976) reported that the pH of precipitation falling on much of Scandinavia was 0.1–0.2 units higher than that which we have measured. Precipitation acidity in our study area is therefore as high or higher than that measured in all areas of the world where damage to aquatic ecosystems has been documented.

A comparison of free hydrogen ion concentration with total acid on four recently collected event samples (Table 3) has demonstrated that a significant proportion of the total acidity (40–60%) is associated with strong acids. Galloway et al. (1976) reported that 50–83% of acidity in precipitation at Ithaca, 89–102% at Hubbard Brook, and 80–86% in the Adirondack Mountains, N.Y., was in the free state. If we subtract

TABLE 2. Mean and range for pH of bulk precipitation at seven stations (12–18) surrounding our study area investigated by J. R. Kramer (unpublished data) in 1973–75, at one station (19) in Killarney Park investigated by Beamish (1976), and at six stations (20–25) in the Sudbury vicinity investigated as part of this study, for comparison with values reported in Table 1. Station numbers refer to Fig. 1.

Station	n	pH Mean	pH Range	H^+ $\mu eq \cdot L^{-1}$
12, Killarney	14	4.06	3.81–7.11	87
13, Sparrow Lake	14	4.22	3.80–5.45	60
14, Lake St. Peter	16	4.04	3.70–5.59	91
15, Traverse Lake	16	4.02	3.66–5.23	95
16, Mattawa	16	4.11	3.84–4.38	78
17, Powassan	15	4.29	3.75–5.83	51
18, Jamot	14	4.18	3.86–6.06	66
19, Lumsden Lake				
Bulk	17	4.4	4.1 –5.3	40
Event	17	4.4	3.7 –5.5	40
20, Nelson Lake	9	4.54[a]	4.2 –5.8	29
21, Mountaintop Lake	6	4.33[a]	4.2 –4.9	47
22, Lohi Lake	15	4.21[a]	3.8 –4.5	62
23, Hannah Lake	13	4.20[a]	3.9 –4.8	63
24, Middle Lake	15	4.33[a]	3.9 –6.3	46
25, Kelly Lake	14	4.43[a]	4.0 –4.9	37

[a]Calculated as volume-weighted arithmetic mean of hydrogen ion concentration ($\mu eq \cdot L^{-1}$).

TABLE 3. pH and acidity of four precipitation events at the Dorset station. The relative importance of the free, carbonate, and "weak acid" components of the total acidity are demonstrated.

Date	pH	Acidity ($\mu eq \cdot L^{-1}$) Total	Free	%	Carbonate	%	"Weak-acid"	%
March 1977 (snow)	4.18	150	60	40	20	13	70	47
June 2, 1977	4.36	85	44	52	23	27	18	21
May 18, 1977	3.69	355	202	57	1	<1	152	43
June 1, 1977	4.26	132	55	42	30	23	47	35

the carbonic acid acidity from the total acidity as Galloway et al. (1976) propose, then 46–71% of the total acidity of the four events was accounted for by free acidity, corroborating the results of Galloway et al. (1976) and Likens and Bormann (1974) that the low pH of precipitation is due to the presence of strong mineral acids.

Sulphate levels of bulk and event samples generally varied between 2 and 4 $mg \cdot L^{-1}$ (42–83 $\mu eq \cdot L^{-1}$) with individual samples having up to 12 $mg \cdot L^{-1}$ (250 $\mu eq \cdot L^{-1}$). All stations had at least one sample in the 6–8 $mg \cdot L^{-1}$ range. The average sulphate concentrations on an equivalent basis were in most cases very close to the mean free hydrogen ion content measured at the stations. We do not have a sufficient number of nitrate, chloride, and ammonium analyses to attempt an ionic balance (Cogbill and Likens 1974; Granat 1972) for the purpose of proportioning the acidity between different chemical species.

The source of the acidity in precipitation falling on south-central Ontario is not easy to determine. Major smelting operations are located to the north and northwest of the study area, and large industrialized urban areas exist to the south and southwest in Canada and the United States. Long range atmospheric transport is such that both these sources likely impact on the study area. The relative significance of the two possible sources is not known at this time. Lafleur and Whelpdale (1977) measured atmospheric SO_4 levels over central Ontario in August 1976 and found that highest levels were associated with southerly regional air flow, indicating that the problem may be an extension of the northeastern USA problem identified by Likens (1976). Further studies are needed to define the principle sources of the acidity of the rainfall in this area.

BUFFERING CAPACITY OF LAKES

The low mineral content of most lakes in south-central Ontario is well known (Ryder 1964; Sparling and Nalewajko 1970; Schindler and Nighswander 1970). Ryder demonstrated that total alkalinity (measured to a pH of 4.5) was generally <500 $\mu eq \cdot L^{-1}$ with the lowest values in the 120–200 $\mu eq \cdot L^{-1}$ range, while Sparling and Nalewajko measured values as low as 70–100 $\mu eq \cdot L^{-1}$ in 1964. As part of a study of the water chemistry of 15 lakes on the Precambrian Shield, we have routinely measured total fixed-endpoint alkalinities of 15 lakes (Table 4) as a crude indication of the lakes' buffering capacities. Levels ranged between 95 and 195 $\mu eq \cdot L^{-1}$ except for Glen Lake, a small lake situated in a pocket of Precambrian sediments with a high calcium and magnesium carbonate content. The total fixed-endpoint alkalinities for the remaining 14 lakes averaged 129 and 143 $\mu eq \cdot L^{-1}$ in the nonstratified and stratified periods, respectively. The total inflection-point alkalinities were measured on one occasion for four lakes; the resulting buffering capacities were much lower than those measured to a pH endpoint of 4.5, being between only 17 and 48% of the latter. That the inflection point of the titration curve was at pH 5.0–5.5 rather than 4.5 is not surprising in view of the very dilute nature of the lakes. The consequence of this, however, is that most of the available data for lakes in this region overestimates the lakes' capabilities for assimilating acidic rain.

Data collected prior to this study are available for 3 of the 15 lakes identified in Table 4. Nicholls (1976) reported that Harp and Jerry lakes had total fixed endpoint alkalinities similar to those reported in Table 4. Unpublished Walker Lake data (Ontario Ministry of the Environment) collected in 1974, however, indicated $\simeq 180$ $\mu eq \cdot L^{-1}$, somewhat greater than the $\simeq 140$ $\mu eq \cdot L^{-1}$ we measured in 1976 but considerably lower than the 400 $\mu eq \cdot L^{-1}$ Michalski (1971) reported for 1971 based on several samples taken on a single date. If the latter figure is accurate, there has been a very significant decline in buffering capacity in Walker Lake between 1971 and 1976.

TABLE 4. Location, mean total fixed endpoint alkalinity, arithmetic mean pH, and sulphate concentration for the whole lake in the nonstratified period and the epilimnion during the stratified period for 15 Haliburton–Muskoka lakes. Alkalinity values in parentheses are based on total inflection point alkalinity measurements.

		Alkalinity ($\mu eq \cdot L^{-1}$)		pH		SO_4 ($\mu eq \cdot L^{-1}$)	
Lake	Location	Non-stratified	Epilimnion	Non-stratified	Epilimnion	Non-stratified	Epilimnion
Blue Chalk	45°12′N, 78°56′W	134	147 (70)	6.48	6.72	158	156
Red Chalk	45°11′N, 78°56′W	135	142 (60)	6.30	6.76	152	151
Jerry	45°23′N, 79°06′W	137	168	6.34	6.72	219	178
Harp	45°23′N, 79°08′W	137	152	6.24	6.70	186	180
Chub	45°13′N, 78°59′W	107	112 (30)	5.98	6.04	185	171
Dickie	45°09′N, 79°05′W	95	117 (20)	5.69	5.91	169	167
Basshaunt	45°07′N, 78°28′W	195	180	6.71	7.27	182	164
Bigwind	45°03′N, 79°03′W	112	130	6.29	6.71	164	164
Buck	45°24′N, 78°59′W	145	160	6.26	6.89	158	167
Crosson	45°02′N, 79°05′W	100	111	5.76	6.03	172	163
Glen	45°07′N, 78°28′W	1190	1050	7.14	8.25	544	484
Gullfeather	45°01′N, 79°06′W	136	112	5.97	6.11	170	167
Little Clear	45°24′N, 79°00′W	175	195	6.45	6.88	177	157
Solitaire	45°23′N, 79°00′W	130	160	6.56	6.86	156	159
Walker	45°23′N, 79°05′W	130	153	6.74	6.74	180	162

Clear Lake (Schindler and Nighswander 1970) was thoroughly investigated in 1967. Total inflection-point alkalinity was reported as 33 $\mu eq \cdot L^{-1}$. We have recently resampled Clear Lake on three occasions (June–August 1977) and measured only 2–15 $\mu eq \cdot L^{-1}$. The very low drainage basin area to lake area ratio (1.4) reported for this lake may explain the very low buffering capacity, since precipitation directly on the lake's surface must be much more important relative to runoff than is usual for lakes in this region.

Without detailed information about the buffering capacity (or cation exchange capacity) of the overburden in lake's watershed, it is impossible to determine the time needed to exhaust the watershed's neutralizing capabilities (McFee et al. 1977). Calculations based on the capability of a lake itself are possible. The buffering capacity of most of the lakes in south-central Ontario is extremely low (10–200 $\mu eq \cdot L^{-1}$). A mean H^+ content of 70–100 $\mu eq \cdot L^{-1}$ in 1.0 m of precipitation results in a loading of 70–100 meq $H^+ \cdot m^{-2} \cdot yr^{-1}$. A lake with buffering capacity of 50 $\mu eq \cdot L^{-1}$ and a mean depth of 10 m has 500 meq $\cdot m^{-2}$, enough to last 5–7 yr. Present buffering capacity, mean depth, and watershed area to lake surface area ratio are all important factors that will determine the eventual effects of acidic rain on each lake, but because the bedrock and overburden of most of the region is very sparingly soluble and provides little buffering, acidification of lakes and streams is likely.

The potential effects of acidic precipitation on Ontario are extremely serious; aquatic and terrestrial damage have been documented in other parts of the world (e.g. Abrahamsen et al. 1976; Odén 1976; Gorham 1976; Odén and Ahl 1970; Almer et al. 1974, etc.). Because a large portion of Ontario is underlain by Precambrian bedrock, the region that can possibly be affected is large. There is no doubt that should current acid loadings continue in south-central Ontario, the acidification of a large number of lakes and streams will follow.

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Metabolic Rate and Energy Expenditure of the Spiny Dogfish, *Squalus acanthias*

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BRETT, J. R., AND J. M. BLACKBURN. 1978. Metabolic rate and energy expenditure of the spiny dogfish, *Squalus acanthias*. J. Fish. Res. Board Can. 35: 816–821.

The metabolic rate of spiny dogfish, *Squalus acanthias*, was determined in both a tunnel respirometer and a large, covered, circular tank (mass respirometer). Swimming performance was very poor in the respirometer, so that a power–performance curve could not be established. Instead, resting metabolic rates were determined, with higher rates induced by causing heavy thrashing (active metabolism). Routine metabolic rates were measured for the spontaneous activity characterizing behavior in the circular tank. For fish of 2 kg mean weight, the metabolic rates at 10°C were 32.4 ± 2.6 SE (resting), 49.2 ± 5.0 SE (routine), and 88.4 ± 4.6 SE (active) mg $O_2 \cdot kg^{-1} \cdot h^{-1}$. Assuming that the routine rate represents a general energy expenditure in nature, this is equivalent to metabolizing about 3.8 kcal $\cdot kg^{-1} \cdot d^{-1}$ (15.9×10^3 J $\cdot kg^{-1} \cdot d^{-1}$).

Key words: dogfish, metabolic rates, energetics, respiration

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Nous avons mesuré le taux métabolique de l'aiguillat commun, *Squalus acanthias*, à la fois dans un respiratomètre tunnel et dans un grand bassin circulaire couvert (respiratomètre de masse). La performance de nage a été très pauvre dans le respiratomètre et il nous a été impossible de construire une courbe puissance–performance. Au lieu de cela, nous avons déterminé les taux métaboliques au repos, des taux plus élevés étant déclenchés en provoquant de vigoureux ébats (métabolisme actif). Nous avons mesuré les taux métaboliques de routine accompagnant l'activité spontanée qui caractérise le comportement dans le bassin circulaire. Chez des poissons de poids moyen de 2 kg, les taux métaboliques à 10°C sont 32.4 ± 2.6 ErT (au repos), 49.2 ± 5.0 ErT (de routine) et 88.4 ± 4.6 ErT (actif) mg $O_2 \cdot kg^{-1} \cdot h^{-1}$. En supposant que le taux de routine représente une dépense d'énergie générale dans la nature, ceci équivaut à métaboliser environ 3.8 kcal $\cdot kg^{-1} \cdot d^{-1}$ (15.9×10^3 J $\cdot kg^{-1} \cdot d^{-1}$).

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RELATIVELY few studies have been made on the metabolic rates of elasmobranchs. Of the 377 records of standard metabolism listed for *Fishes* in Biological Handbooks (Altman and Dittmer 1974) only 10 (2.8%) occur for cartilaginous fishes (Class: Chondrichthyes, Subclass: Elasmobranchii).

No systematic study of other than resting metabolic rates has been conducted on the spiny dogfish, *Squalus acanthias* syn. *suckleyi* (Pritchard et al. 1958). Because of the great abundance of this species, and its reputation for feeding on valuable commercial fish including herring, salmon, and crab (Hart 1973; Jones 1976), an assessment of the general energy requirements was desirable. Experiments were therefore conducted to determine the various levels of metabolic rate (standard, routine, and active) accompanying the corresponding levels of activity (resting, spontaneous swimming, and maximum sustained activity) at a normal environmental temperature (10°C).

The particular purpose of this study was to estimate the likely annual food intake of dogfish to support their metabolic energy requirements. The metabolic rates of other elasmobranchs are reviewed and compared with those of the dogfish.

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Materials and Methods

THE FISH

Dogfish caught on longlines in Northumberland Channel, B.C., were held in tanks at 10 ± 1°C for 1–6 wk before use. No feeding was attempted. Although a variety of sizes was available, for reasons described below only those weighing approximately 2 kg and about 82 cm long were used (Table 1). Data on 23 fish were obtained. No anesthetic was applied; the fish could be grasped by the caudal peduncle and quickly inserted in either one of the two respirometers used.

TABLE 1. Length, weight, and sex of individual dogfish used in the tunnel respirometer, and the average length, average weight, and sex ratio of the groups of six fish tested in the mass respirometer.

Apparatus	Fish no.	Length (cm)	Wt (kg)	Sex
Tunnel respirometer	1	75.6	1.52	♂
Tunnel respirometer	2	80.0	1.92	♂
Tunnel respirometer	3	79.2	1.82	♂
Tunnel respirometer	4	79.9	1.95	♂
Tunnel respirometer	5	80.7	2.06	♂
Mass respirometer	Group 1	86.3	2.40	6♂/0♀
Mass respirometer	Group 2	81.0	1.91	6♂/0♀
Mass respirometer	Group 3	80.7	1.87	4♂/2♀

TUNNEL RESPIROMETER

Following the work on metabolic rates of salmon (reviewed in Brett and Glass 1973) it was expected that the large tunnel respirometer (Bell and Terhune 1970), with a volume of 123 L and a tunnel section of 150-cm length by 20-cm diameter, would be suitable for dogfish. The first objective was the development of a power–performance curve, using the usual stepwise procedure of incremental increases in swimming speed while determining the accompanying rates of oxygen consumption. However, at no time was it possible to obtain a continuous, uninterrupted period of swimming at any prescribed velocity. Fish that were small enough would turn around and become jammed on the downstream, electrified screen. Only larger fish, with their pectoral fins touching the tunnel wall, could be used. Possibly because of this restriction, the fish would end up twisting and writhing as the velocity was increased and they repeatedly touched the low voltage shocker. No fish of the particular dimensions that permitted free swimming without wall contact (and yet could not turn around) were available. At low velocities the larger fish would rest and periodically start spontaneous activity with slow undulating movements building up to short, restless periods of writhing — possibly a form of escape behavior. The period of rest following these episodes lasted from 3 to 5 h.

As a consequence of this irregular behavior it was decided to monitor the spontaneous activity while intermittently obtaining hour-long measurements of oxygen consumption, and to record the accompanying respiratory frequencies (opercular beats). Activity levels were assigned to *high*, *medium*, or *low* (resting) states before the terminal oxygen sample was collected. In addition, before removing each of the five fish so studied, a 15-min period of maximum thrashing activity was induced by multiple stimulation using strong light, sound, and electrical shocking of the tail. From the oxygen debt so induced the recovery period was recorded and a means of estimating active metabolism obtained (elaborated under Results).

All oxygen determinations were duplicate titrations using the Winkler method, with the thiosulphate solution standardized weekly. Exchange water maintained oxygen levels between 85 and 95% saturation. Salinity was 28‰.

MASS RESPIROMETER

Because of the behavioral difficulties experienced with the tunnel respirometer, it was decided to use the simple "mass respirometer" technique employed by Saunders (1963) when studying routine and standard metabolic rates of Atlantic cod. Groups of six dogfish of similar size (Table 1) were placed in a 1450-L, circular fiberglass tank (2-m diameter, 1-m depth) and permitted to swim freely. Their level of activity was very similar to that observed for dogfish in a large outdoor netting enclosure (described in Jones 1976). To eliminate diffusion of oxygen from the air, a polyethylene sheet (1 mm thick) was stretched across the water surface and held tightly to the wall with clamps. By flooding the plastic surface with a layer of cooler water the slight heating from a submerged circulation pump was counteracted during closed-circuit periods.

Initially the fish swam around and nosed against the plastic sheet, but showed no sign of particular excitement. After a few minutes they settled down to resting or cruising around the tank. The number of fish resting was recorded periodically, and usually involved four of the six fish. In general the fish were apparently more active during the first 2 d of testing than the following 2 d.

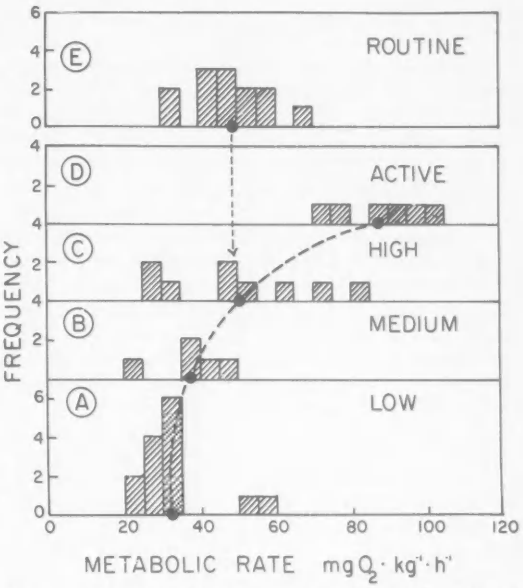

FIG. 1. Frequency histograms of metabolic rates grouped according to their occurrence within ranges of 5 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ (from 20 to 105 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$). They are displayed according to activity level in the tunnel respirometer (A–D) and mass respirometer (E). Mean rates are shown by (●). Broken lines have no significance other than to show the increasing trend (A–D), and the relative position of the routine rate (E) corresponding to "high."

Results and Discussion

SPONTANEOUS ACTIVITY

Tunnel respirometer — The mean metabolic rate rose from a classified *low* of 32.4 ± 2.6 SE, through a *medium* of 36.8 ± 4.3 SE to a *high* of 50.5 ± 6.4 SE

(Fig. 1). Although there was a small, significant[1] shift upwards in the mean metabolic rates between *low* and *medium* it is apparent that there was no major difference in the respective rates recorded; the range of values was even slightly greater among spontaneous activity records classed as *low* than those classed as *medium*. Since continuous monitoring of daily activity throughout the 24 h was not conducted, it is apparent that some observations classed as *low* had likely followed an unobserved period of *medium* and even *high* spontaneous activity. Hence the categories are all forms of routine metabolism with the lowest approaching true standard metabolism (= basal) but not that of a completely resting fish, so that the minimum mean values determined can only be considered as provisionary standard metabolic rates, with the true standard likely falling between 20 and 30 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$.

Mass respirometer — The routine metabolic rate so recorded was 49.2 ± 5.0 SE. This is very comparable to the metabolic rate classed as *high* in the tunnel respirometer. Since at least four out of the group of six fish in the large tank were usually swimming when observations were made it is apparent that at times all six were in an active state. A metabolic rate of about 50 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ would be a representative value for normal energy expenditure in nature. Only activity levels associated with migration, attack, and escape would push the rate over this general level.

Induced Activity and Oxygen Debt

Following fatigue from intense stimulation, the metabolic rate subsided in an exponential fashion (Fig. 2). The fish rested at the bottom of the tunnel ventilating deeply in the slow stream of water flushed over them. By the end of the 3rd h spontaneous activity began in two of the four fish tested, causing the average oxygen consumption rate to level off about 25% above the resting rate. Since a 20-min closed-circuit interval was used to determine each point depicted in Fig. 2, an extrapolation to zero time indicates that for this sample the active metabolic rate approximates 100 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$.

The rate of recovery of yearling sockeye salmon, *Oncorhynchus nerka* (average 50 g), was approximately the same as that for the dogfish, terminating after 3 h, independent of temperature (Brett 1964). Because of the opportunity for ram ventilation in salmon (at high swimming speeds) the active rate of oxygen consumption was found to be almost twice the maximum rate of consumption during deep ventilation at rest. This phenomenon would not likely apply to the inferior mouth and buccal anatomy of the dogfish although some reduction in respiratory rate has been noted for two species of Japanese sharks when swimming (Clark and Kabasawa 1977).

The total oxygen debt incurred can be determined by the area under the curve extrapolated to the level of the standard metabolic rate (Fig. 2). It amounted to 105 mg O_2/kg. A similar calculation for sockeye salmon

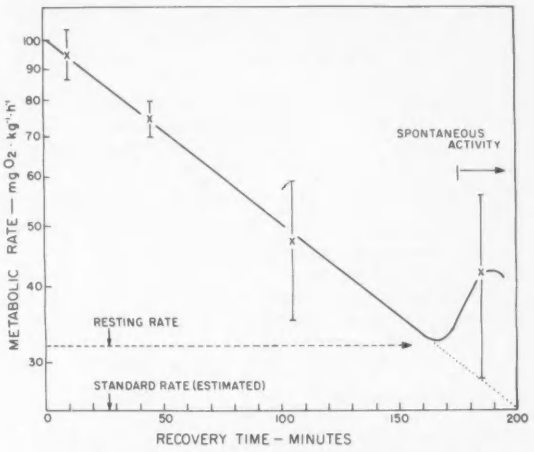

FIG. 2. Rate of oxygen consumption (log scale) of four dogfish during recovery from oxygen debt induced by strong stimulation causing fatigue. About 3 h after exhaustion some spontaneous activity commenced, elevating the metabolic rate of the last record (at 185 min). Mean rates ± 1 SD shown. The standard rate is an estimated level for use in determining total oxygen debt.

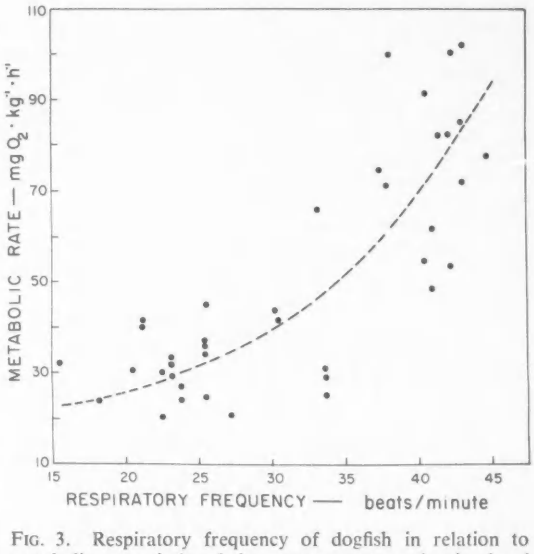

FIG. 3. Respiratory frequency of dogfish in relation to metabolic rate induced by spontaneous and stimulated activity in a tunnel respirometer. Water velocity through tunnel respirometer was constant at 5 cm/s during measurements. Broken line is described by the equation — $\log_{10} Y = 1.024 + 0.0198 X$, linearizing the transformed data, where Y = mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ and X = beats/min (determined by least squares).

[1]From *t*-test for two groups of unequal sizes, $t = 3.7$; $t_{0.01} = 2.9$ (Snedecor and Cochran 1968).

TABLE 2. Metabolic rates of elasmobranchs (Chondrichthyes) recorded in the literature, and listed in order of date published. See Winberg 1956 for those references so indicated. Note that oxygen has been expressed in milligrams not millilitres. Also, that "resting" metabolic rate refers to the immediate observed state and is not necessarily equivalent to standard metabolic rate.

Species	Wt ± SD or range (g)	Acclimation temp ± avg range (°C)	Metabolic rate ± SD		No. of cases (*n*)	Comments	Reference
			Resting (mg $O_2 \cdot kg^{-1} \cdot h^{-1}$)	Routine (mg $O_2 \cdot kg^{-1} \cdot h^{-1}$)			
Scyllium catulus	440	15	55	—	1	Recorded in table 16 of Winberg (1956).	Jolyet and Regnard (1877).
Raja torpedo (skate)	315–410	14	67	—	2	Recorded in table 14 of Winberg (1956).	Bounhiol (1905).
Scyliorhinus stellaris (spotted dogfish)	660–685	18.5	83	—	2	Recorded in table 16 of Winberg (1956).	Bounhiol (1905).
Scyllium cassicula (or *canicula*?)	14–24	13	—	159	2	Recorded in table 16 of Winberg (1956). Assumed to be a high routine metabolic rate.	Buytendijk (1910).
S. cassicula (or *canicula*?)	150–260	13	—	99	3	Recorded in table 16 of Winberg (1956). Assumed to be an average routine rate.	Buytendijk (1910).
S. catulus	19–24	14	—	204	2	Recorded in table 16 of Winberg (1956). Assumed to be at a high routine metabolic rate.	Raffy (1932).
Squalus suckleyi[a] (spiny dogfish)	3520 ± 2400	13 ± 1	53.2 ± 6.4	—	38	Quiescent. Starved 2 d. All ♀. Smallest and largest fish omitted here, apparently aberrant.	Pritchard et al. (1958).
S. suckleyi[a] (spiny dogfish)	350	11	60.9	—	10	Surgically cannulated in branchial artery (2 wk or more).	Lenfant and Johansen (1966).
Scyliorhinus stellaris (larger spotted dogfish)	1860 ± 86	17 ± 2	57 ± 21	—	6	Held 3–15 d. Anesthetized and restrained in tanks with tail cut off (for catheterizing blood vessels).	Piiper and Schumann (1967).
S. canicula (rough hound)	150–600	13 ± 1	60–80	114	(5)?	Varied flow rate over restrained fish in a cylindrical tube. Maximum obtained = 136 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$.	Hughes and Umezawa (1968).
S. stellaris (larger spotted dogfish)	2180 ± 50	16 ± 1	55 ± 15	—	11	Not anesthetized. Restrained with tail cut.	Baumgarten-Schumann and Piiper (1968).
S. canicula (rough hound)	560 ± 1050	7	29.7 ± 8.7	—	7	Restrained and surgically cannulated; 16 h recovery allowed in respirometer.	Butler and Taylor (1975).
	560 ± 1050	12	39.9 ± 10.2	—	8		
	560 ± 1050	17	64.3 ± 12.7	—	7		
Hemiscyllium plagiosum (lip-shark)	360–1400	23 ± 1	68.6 ± 6.0	—	(8)?	Unfed, 1 wk adaptation to 33‰ seawater; 5 L, Perspex box respirometer used.	Chan and Wong (1977).
Squalus acanthias (spiny dogfish)	2000	10	32.4 ± 9.4	49.2 ± 18	13	Tunnel and mass respirometers used.	Brett and Blackburn (this paper).

[a]American Fisheries Society lists as *Squalus acanthias*.

(50 g) at 10°C was 457 mg O_2/kg. Although size difference between the samples of the two species studied would have some effect, the fact that the dogfish can only tolerate one fourth of the debt sustained by salmon is indicative of the limited metabolic capacity of this comparatively sluggish fish. The difference is further supported by the fact that the active metabolic rate of a 2-kg sockeye at 10°C would be about 600 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ (Brett and Glass 1973), whereas that of 2-kg dogfish would hardly exceed 100 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$.

RESPIRATORY FREQUENCY AND OXYGEN CONSUMPTION

The average number of beats of the gill openings rose from about 20/min at the resting level to a maximum of 45/min at the highest rate of oxygen consumption (Fig. 3). There was a geometric increase in consumption for an arithmetic increase in frequency. This indicates that the volume exchange and the extraction efficiency of oxygen per unit volume passed over the gills were relatively greater for each increase in beat rate. It has been demonstrated that an increase in *volume* across the gills of restrained elasmobranchs results in an increase in oxygen extraction (e.g. Hughes and Umezawa 1968; Piiper and Schumann 1967). However, in the foregoing reports variation in respiratory *frequency* with increasing rate of oxygen consumption has tended to be minimal (±3 beats/min).

The trend of the curve in Fig. 3 adds further support for the supposition that the standard metabolic rate lies between 20 and 30 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$.

Metabolic Energy Requirements

The oxycalorific equivalent for respired oxygen in teleosts is considered to be 3.25 cal/mg O_2 (Elliott and Davison 1975). Assuming this to be an appropriate value for dogfish, the routine metabolic expenditure would be 160 cal·kg^{-1}·h^{-1}, or 3.84 kcal·kg^{-1}·d^{-1} (for a 2-kg fish at 10°C). Carnivorous fish feeding on other fish excrete an average of 27% of the energy of ingested food (Brett and Groves 1978). On this basis the dogfish would have to consume 5.26 kcal·kg^{-1}·d^{-1} to provide for routine metabolism. If the caloric content of the prey consumed by dogfish (e.g. herring, salmon) is 1.3 kcal/g of wet weight then a 1-kg dogfish would consume about 4 g·kg^{-1}·d^{-1}. Applying this as the average for the year, a 2-kg dogfish would eat 1.5 times its own weight solely for routine metabolic energy. It would not be unfounded to increase this annual figure to 2 times the body weight to take into account the additional energies required for the normal events of attack and escape in the activities of feeding and surviving. By comparison, a salmon of similar weight would be expected to consume 3–4 times as much as a dogfish for metabolic purposes (e.g. sockeye salmon at 10°C; see Brett 1970).

General Metabolic Rates of Elasmobranchs

A survey of the various records of metabolic rates of elasmobranchs has been compiled in Table 2. For all cases of "resting" metabolism ($n = 13$) involving seven species the average rate was 57 mg O_2·kg^{-1}·h^{-1} (range = 30–83 mg O_2). This was at an average temperature of 15°C (range = 7–18°C) and an average weight of about 900 g (range = 14–3520 g). The rate is closest to the routine rate (49 mg O_2·kg^{-1}·h^{-1}) for the dogfish determined at 10°C in our experiments. If the latter rate is adjusted upward to a temperature of 15°C (using a Q_{10} of 2.2) the routine rate for dogfish would be about 75 mg O_2·kg^{-1}·h^{-1} suggesting that the general case for "resting" metabolism lies, as expected, somewhere between the true standard and routine rates. A reasonable estimate for general standard rate of elasmobranchs would be about 40 mg O_2·kg^{-1}·h^{-1} at 15°C.

For the five cases listed as "routine" metabolism in Table 2, at an average temperature of 13°C and weight of 530 g (range = 14–2000 g), the average metabolic rate was 125 mg O_2·kg^{-1}·h^{-1} (range = 49–204 mg O_2). If the single record of 204 mg O_2·kg^{-1}·h^{-1}, which is exceptionally high, is removed the average becomes 106 mg O_2·kg^{-1}·h^{-1} (at 13°C). This approximates the active metabolic rate of dogfish at 10°C.

It can be concluded that for the species of cartilaginous fishes which have been chosen for physiological studies the general metabolic levels are among the lowest of all fishes. The bony fishes (teleosts, Class: Osteichthys) have an average standard rate of 90 mg O_2·kg^{-1}·h^{-1}, with a range of 29–229 mg O_2 (Brett and Groves 1978). Active metabolic rates of fast-swimming teleosts approach 1000 mg O_2·kg^{-1}·h^{-1}, with the most sluggish fish only achieving a maximum rate of about 160 mg O_2·kg^{-1}·h^{-1} (Brett 1972). The elasmobranchs are on a par with these inactive forms. It is of importance, however, to recognize the sort of selection that has been exercised in the choice of most cartilaginous species — ease of handling and resistance to the stress of surgical manipulation. The fact that some elasmobranchs have developed the advanced streamlining and warm-bodied temperatures of some highly evolved teleosts (Carey et al. 1971) attests to the likely presence of great metabolic capacity. It will be no small challenge to obtain systematic records on these more active members of the Class Chondrichthyes.

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Prevention and Treatment of Nitrite Toxicity in Juvenile Steelhead Trout (*Salmo gairdneri*)

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WEDEMEYER, G. A., AND W. T. YASUTAKE. 1978. Prevention and treatment of nitrite toxicity in juvenile steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 35: 822–827.

The efficacy of mineral salts, pH, and tetramethylthianine (methylene blue) treatment in reducing the acute toxicity of nitrite to fingerling steelhead trout (*Salmo gairdneri*) was determined using a static bioassay system at 10°C. The acute toxicity (96-h LC50) was reduced by a factor of about 24 for 5-g steelhead and 13 for 10-g fish when the total water hardness was increased from 25 to 300 mg/L (as $CaCO_3$). NaCl or $CaCl_2$ additions (0–200 mg/L) reduced toxicity by a factor of up to 3 for NaCl and 50 for $CaCl_2$. Increasing the pH from 6.0 to 8.0 decreased toxicity by a factor of about 8 for the smaller and 3 for the larger fish. Methylene blue at 0.1 or 1.0 mg/L was effective in decreasing acute toxicity. For alleviating methemoglobinemia, removing the fish to freshwater for 48 h was about as effective as 1.0 mg/L methylene blue. Chronic exposure in soft water to 0.03 mg/L NO_2-N for 6 mo caused no significant growth reduction, gill histological changes, hematological dyscrasias, or impaired ability of the smolts to adapt to 30‰ seawater and grow for an additional 2 mo.

Key words: nitrite, toxicity, fish, methylene blue, pH, salts, acute toxicity, chronic toxicity

WEDEMEYER, G. A., AND W. T. YASUTAKE. 1978. Prevention and treatment of nitrite toxicity in juvenile steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 35: 822–827.

Nous avons mesuré l'efficacité des sels minéraux, du pH et de la tétraméthylthianine (bleu de méthylène) comme traitements visant à réduire la toxicité aiguë du nitrite pour des fingerlings de truite steelhead (*Salmo gairdneri*), utilisant un système d'analyses biologiques statiques à 10°C. Si l'on fait passer la dureté totale de l'eau de 25 à environ 300 mg/L (comme $CaCO_3$), la toxicité aiguë (CL50 de 96 h) diminue d'une facteur d'environ 24 chez les truites de 5 g et de 13 chez les truites de 10 g. Des additions de NaCl ou de $CaCl_2$ (0–200 mg/L) réduisent la toxicité d'un facteur allant jusqu'à 3 pour le NaCl et 50 pour le $CaCl_2$. Un pH passant de 6.0 à 8.0 diminue la toxicité d'un facteur d'environ 8 pour les petits et de 3 pour les grands poissons. Le bleu de méthylène à 0.1 ou 1.0 mg/L est un agent efficace de diminution de la toxicité aiguë. Cependant, le transfert des poissons dans de l'eau douce pendant 48 h est tout aussi efficace qu'un traitement à 1.0 mg/L de bleu de méthylène pour les soulager de la méthémoglobinémie. Une exposition chronique d'une durée de 6 mo à 0.03 mg/L de NO_2-N dans de l'eau douce ne cause aucune diminution significative de croissance, changement histologique de la branchie, trouble de la crase sanguine ou capacité amoindrie des smolts à s'adapter à de l'eau de mer à 30‰ et à croître durant une période supplémentaire de 2 mo.

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THE increasing need for intensive fish culture coupled with restrictions on available water supplies has led to the construction of hatcheries in which up to 95% of the hatchery effluent is recirculated. Water reuse systems and biological filters are used to achieve nitrification of ammonia as well as control of pH, temperature, and dissolved oxygen. However, a variety of factors, such as heterotrophic overgrowth because of organic carbon buildup, can cause dynamic imbalances in the desired autotrophic bacterial populations. Increased nitrite levels above design specifications are not uncommon.

One major toxic physiological effect of nitrite is methemoglobinemia, which can severely compromise fish health even if mortalities do not occur. Unfortunately, the literature values for the acute toxicity of nitrite are somewhat conflicting (see summary in Russo and Thurston 1977) and do not include the economically important steelhead trout (*Salmo gairdneri*). Maximum safe chronic exposure levels are even more poorly defined. The variations in reported acute toxicity are pre-

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TABLE 1. Mineral salt mixtures used to achieve designated total hardness levels (Marking 1969). Resulting Cl^- and pH values are also given.

Water designation	Total hardness (mg/L $CaCO_3$)	Salts added (mg/L)				pH	Cl^- (mg/L)
		$NaHCO_3$	$CaSO_4 \cdot 2H_2O$	$MgSO_4$	KCl		
Soft	50	48	30	30	2	6.8	1.0
Hard	100	192	120	120	8	7.3	4.2
Very hard	300	384	240	240	16	7.8	8.4

TABLE 2. Effect of total hardness (as $CaCO_3$) and fish size on acute toxicity of nitrite to juvenile steelhead trout, 10°C; duplicate static bioassays, 20 fish per group.

Hardness (mg/L)	Chloride (mg/L)	pH	Designation	96-h LC50 and 95% confidence limits (mg/L NO_2-N)	
				5-g steelhead	10-g steelhead
25	1.9	6.2	Very soft	0.5 (0.4–0.6)	0.9 (0.8–1.1)
50	1.4	6.8	Soft	0.5 (0.3–0.6)	1.9 (1.7–2.2)
150	4.2	7.3	Hard	4.7 (3.6–6.1)	5.8 (5.0–6.7)
300	8.4	7.8	Very hard	10.3 (8.5–12.5)	12.1 (10.7–13.8)

sumably caused by differences in fish size and species, and by water chemistry effects, such as the protection afforded by Cl^- reported by Perrone and Meade (1977).

The present study was carried out to develop (1) acute and chronic toxicity data for juvenile steelhead trout, (2) guidelines for the manipulation of water chemistry to prevent nitrite toxicity in hatcheries, and (3) treatment methodology to be used in the event nitrite poisoning does occur. Steelhead trout were chosen as the test species because of their importance in anadromous fishery programs and because no toxicity information was available except for the taxonomically related rainbow trout.

Materials and Methods

Steelhead trout, 5–10 g, were acclimated to the laboratory in 10°C, soft water (25 mg/L total hardness as $CaCO_3$) for a minimum of 30 d before use. All fish were given an initial 1 h, 200 ppm prophylactic formalin treatment and fed a terramycin-medicated Oregon moist pellet diet for 2 wk to eliminate external parasites and subclinical bacterial infections. Standard toxicity testing procedures were followed with duplicate 10 fish groups per nitrite level tested (EPA 1975).

For the acute tests, static 96-h LC50 bioassays were run at 10°C to determine the effect of fish size, mineral salt additions, and pH. The bioassay water was changed daily by siphon to minimize stress effects and the dissolved oxygen (D.O.) maintained near 10 mg/L by aeration. The mineral salt mixtures recommended by Marking (1969) were used to achieve the desired water hardness (Table 1). For the pH tests, phosphate buffer was added to the bioassay water at 0.04 M/L to hold the pH at the desired level. The pH was confirmed daily when the bioassay water was changed.

The chemical composition of the bioassay water was 25 mg/L total hardness (as $CaCO_3$), pH 6.2, 8 mg/L Ca^{++}, 1.2 mg/L free CO_2, 2.3 mg/L Cl^-, 1.2 mg/L Mg^{++}, 0.01 mg/L NH_3-N, 0.01 mg/L NO_3-N, 8–10 mg/L D.O. There was no detectable nitrite.

For the partial chronic tests, the 0, 0.015, 0.030, 0.060 mg/L NO_2-N levels were tested over a 6-mo rearing period in a flow-through system. The levels were confirmed by weekly chemical analyses. Histological and hematological changes including methemoglobinemia, and growth disturbances were used to evaluate sublethal effects on fish health. In addition, ability to adapt to seawater and continue to grow normally for 2 mo after smoltification was evaluated.

Peripheral blood smears, kidney tissue imprints, and hemoglobin, methemoglobin, and nitrite determinations were done following the standard methods outlined in Wedemeyer and Yasutake (1977). Histological sections were prepared and stained with hematoxylin and eosin.

96-h LC50 values were determined graphically by probit analysis and 95% confidence intervals calculated by the Litchfield-Wilcoxon method (Litchfield and Wilcoxon 1949).

Results and Discussion

Acute Toxicity

The 96-h LC50 of nitrite to juvenile steelhead trout was influenced by total hardness, NaCl or $CaCl_2$ levels, pH, and fish size. Mineral salt additions sufficient to increase the total hardness to 150 or 300 mg/L (as $CaCO_3$) gave substantial protection against nitrite to both the 5- and 10-g steelhead (Table 2). In very hard water the toxicity of nitrite to the smaller fish was reduced by a factor of approximately 20. The larger steelhead were also somewhat more resistant to nitrite than were the smaller fish, except in the harder (150 and 300 mg/L) water where the 95% confidence intervals began to overlap making the differences minor.

Because the harder bioassay waters were also the more alkaline, the role of pH in preventing acute nitrite toxicity was evaluated separately. To minimize salt ef-

TABLE 3. Effect of pH on the acute toxicity of nitrite to juvenile steelhead trout, 10°C, soft water, 0.04 M phosphate buffer, 1.9 mg/L Cl^-; duplicate static bioassays, 20 fish per group.

	96-h LC50 and 95% confidence limits (mg/L NO_2-N)	
Water pH	5-g steelhead	10-g steelhead
6.0	0.3 (0.2–0.4)	1.4 (1.1–1.7)
7.0	1.5 (1.2–1.8)	2.3 (1.0–2.9)
8.0	2.5 (2.3–2.8)	3.6 (3.1–4.2)

fects, a relatively dilute 0.04 M phosphate buffer was used to maintain the soft (25 mg/L) bioassay water at the desired pH. Increasing the water pH to 8 reduced nitrite toxicity by a factor of about 8 for the 5-g steelhead and 3 for the larger fish (Table 3). This lessened toxicity may be partially explained by the fact that nitrite in water is in a pH and temperature dependent equilibrium with the more toxic un-ionized form, nitrous acid (Colt and Tchobanoglous 1976). The calculated percent NO_2^- present as nitrous acid (HNO_2) at pH 6 and 8, 10°C, is 0.29 and 0.0029%, respectively.[1] However, the amount of the more toxic, un-ionized HNO_2 does decrease a hundredfold as the pH increases from 6 to 8 which is presumptive evidence that part of the protective effect of both hard and alkaline waters arises because formation of the more toxic HNO_2 is suppressed.

The mineral salt mixtures somewhat increased the total Cl^- levels, as well as the pH (Table 2), which may also have contributed to the protective effect (Perrone and Meade 1977). To evaluate the possibility that the salt mixture could thus be simplified without losing protective effectiveness, 96-h LC50 tests were run adding only NaCl or $CaCl_2$. Both salts protected 15-g steelhead against nitrite toxicity but $CaCl_2$ was the more effective (Table 4). A $CaCl_2$ level as low as 25 mg/L reduced nitrite toxicity by a factor of about 12 whereas this level of NaCl reduced the toxicity by a factor of less than 2. Some of this protection is undoubtedly attributable to the chloride ion effect discovered by Perrone and Meade (1977). However, it seems likely that the Ca^{++} ion is also involved because both salts contain about the same percent Cl^- (61 vs. 64%). Supporting evidence for this is the seawater inhibition of nitrite toxicity to chinook salmon (*O. tshawytscha*) reported by Crawford and Allen (1977) in which Ca^{++} ion was strongly implicated.

Experience has shown that, in general, fish sensitivity to toxicants is inversely proportional to size and the present results with nitrite vs. steelhead trout size are in agreement with this (Tables 2, 3). However, the harder waters or the soft water buffered to pH 8 considerably diminished the fish size effect and the differences in 96-h LC50 became relatively small. Russo et al. (1974) and Smith and Williams (1974) reported that small (rainbow) trout were somewhat more resistant to nitrite than were larger fish.

[1] $\%\ HNO_2 = \frac{100}{1 + \text{antilog}(pH - pK_{HNO_2})}$

pK_{HNO_2} at 5, 10, 15, 20°C = 3.505, 3.463, 3.423, 3.384, respectively.

TABLE 4. Protective effect of NaCl and $CaCl_2$ additions in reducing the toxicity of nitrite to 15-g steelhead trout, 10°C, soft water, duplicate bioassays, 20 fish per group.

Salt level (mg/L)	Total chloride present (mg/L)	96-h LC50 and 95% confidence limits (mg/L NO_2-N)
	NaCl	
0	1.0	0.54 (0.45–0.66)
25	18.1	0.91 (0.78–1.1)
50	33.3	0.78 (0.63–0.97)
100	63.7	0.97 (0.64–1.5)
200	124.4	1.5 (0.88–2.61)
	$CaCl_2$	
0	1.9	0.64 (0.54–0.76)
25	18.9	7.3 (6.2–8.5)
50	34.9	10.0 (8.4–11.9)
100	66.9	22.7 (17.5–29.7)
200	130.5	31.2 (26.0–37.6)

TABLE 5. Mean (SD) hemoglobin and methemoglobin levels in juvenile steelhead trout exposed for 6 mo to nitrite, 10°C, 120-fish samples; * indicates significant increase ($P = 0.05$).

		Methemoglobin	
NO_2-N (mg/L)	Hemoglobin (g/100 mL)	g/100 mL	% of total Hb
0 (controls)	6.6 (1.5)	0.10 (0.07)	1.5 (1.8)
0.015	7.5 (0.9)	0.20 (0.1)	2.7* (3.1)
0.030	7.6 (0.9)	0.25 (0.2)	3.4* (4.1)
0.060	7.5 (0.7)	0.29 (0.2)	3.6* (3.9)

CHRONIC TOXICITY

Nitrite exposure during a 6-mo rearing period, at 0.015, 0.030, or 0.060 mg/L NO_2-N caused a statistically significant though biologically mild methemoglobinemia (Table 5). Although not lethal in itself, 3–4% met-Hb is still somewhat above the usual 1–2% baseline level in unexposed steelhead and would slightly reduce blood oxygen carrying capacity. However, in the usual sedentary hatchery environment, this degree of methemoglobinemia would not be expected to affect growth noticeably, or ability of the fish to adapt to seawater and continue to grow normally after smoltification. Regression of growth in fresh or salt water on freshwater nitrite exposure level showed that there was no significant correlation ($P = 0.05$) (Table 6). Also, conversion to 30‰ seawater (over a 48-h period) caused no mortalities.

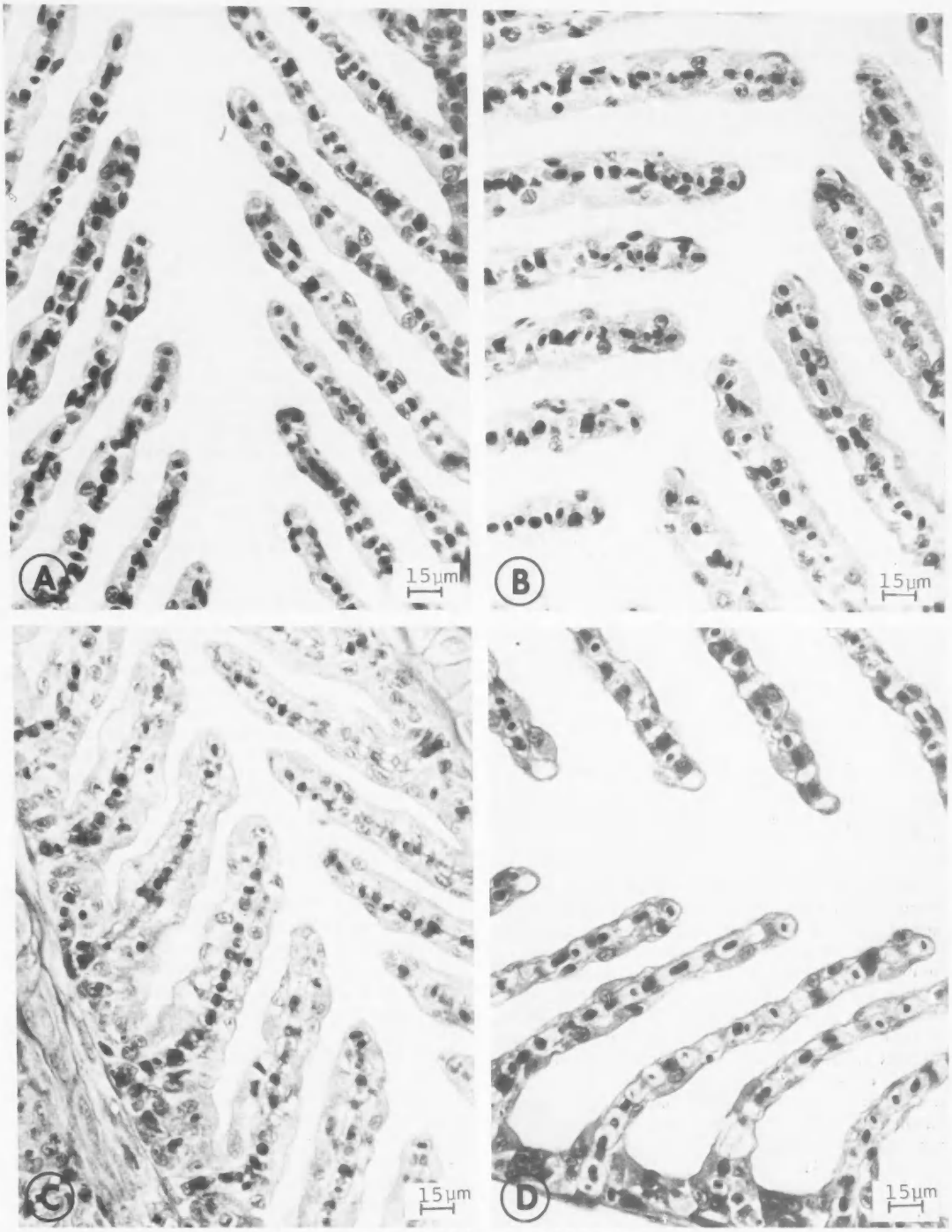

FIG. 1. Steelhead trout gill lamellae after exposure to 0.060 mg/L nitrite-N. Hematoxylin and eosin stain. A, Unexposed control; B, 4-wk exposure. Note hypertrophic lamellar epithelium; C, 6-wk exposure. Note hypertrophic lamellar epithelium accompanied by cloudy swelling of the epithelial cells; D, 28-wk exposure. Most of the test fish had recovered and exhibited little or no lamellar epithelial change.

TABLE 6. Effect of chronic nitrite exposure over a 6-mo rearing period in freshwater, on growth and ability of steelhead to adapt to seawater and grow for an additional 2 mo. There was no significant correlation ($P = 0.05$) between growth and nitrite exposure.

Chronic exposure level (mg/L NO_2-N)	% weight gain		
	Freshwater (6 mo)	Seawater (2 mo)	Total (8 mo)
0 (controls)	61	59	120
0.015	44	59	103
0.030	53	56	109
0.060	51	66	117

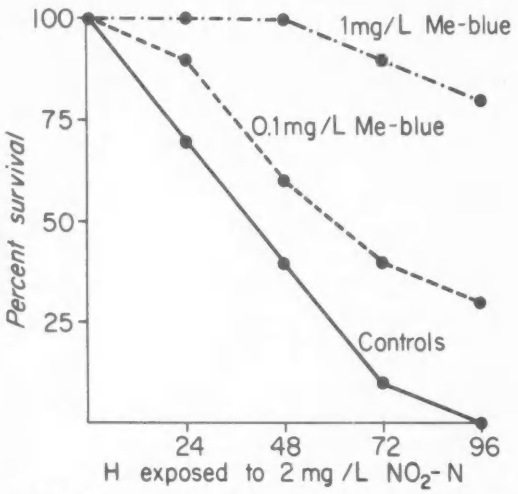

FIG. 2. Efficacy of 0, 0.1, or 1.0 mg/L methylene blue additions in preventing steelhead mortalities during exposure to 2 mg/L NO_2-N, 10°C.

Peripheral blood smears and anterior kidney imprints revealed no hematological abnormalities at any of the nitrite levels tested. Hemorrhagic and necrotic lesions in the thymus, and the atypical discolorations seen by Smith and Williams (1974) in acutely intoxicated rainbow trout, were also not apparent. However, at the 0.060 mg/L exposure level, the gill epithelium showed varied degrees of minimal hypertrophy, hyperplasia, and lamellar separation after 3-wk exposure and through the 7th wk (Fig. 1A–C). After 7 wk the changes were seen less frequently, suggesting that adaptation was occurring. After 28-wk exposure most of the test fish had recovered and showed little or no lamellar epithelial change (Fig. 1D).

TREATMENT OF TOXICITY

Because of biofilter malfunctions, nitrite intoxication occasionally will occur and treatment will be necessary. Of the two traditional means of alleviating methemoglobinemia, methylene blue and high dietary ascorbate (Cameron 1971), methylene blue additions were chosen for evaluation in this study. Methylene blue by injection (10 mg/kg intraperitoneally) has been used successfully by Bortz (1976). Figure 2 illustrates the protection that methylene blue added to the bioassay water at 0.1 and 1.0 mg/L offers against nitrite toxicity. Unfortunately, methylene blue at 5 mg/L is a known nitrification inhibitor (Collins et al. 1975) and even these lower levels would be suspect in biofilter reuse systems. Thus, the alternative method of transferring nitrite intoxicated steelhead to a separate methylene blue batch treatment tank was evaluated. As shown in Fig. 3 for the 0, 0.1, or 1.0 mg/L methylene blue levels, removing nitrite-intoxicated fish to freshwater was about as effective as 0.1 mg/L treatments. However, 1 mg/L methylene blue did dramatically reduce the methemoglobinemia during the first few hours which would probably be a critical advantage in treating severely poisoned fish. In these tests there were no mortalities at any of the treatment levels.

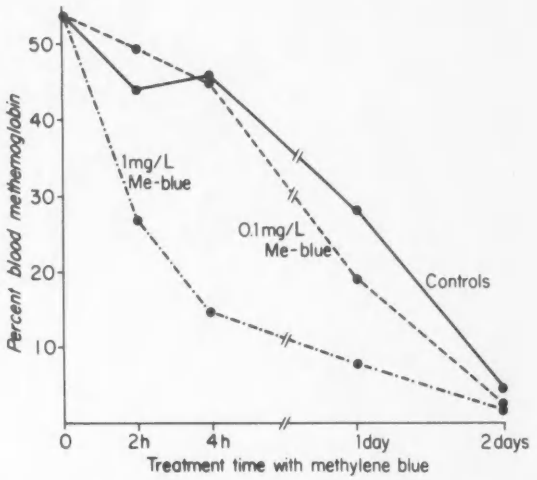

FIG. 3. Efficacy of methylene blue at 0, 0.1, 1.0 mg/L in treating methemoglobinemia in 15-g steelhead trout intoxicated with 2 mg/L NO_2-N, 10°C. Each value is the mean of three duplicate runs, 15 fish per sample.

The fact that steelhead can clear methemoglobin so quickly lends weight to the suggestion by Brown and McLeay (1975) that an erythrocytic Met-Hb reductase enzyme system exists in salmonids.

In summary, mineral salt additions and pH control can be used to reduce the acute toxicity of nitrite to juvenile steelhead trout in soft water. Calcium chloride alone, at 50 mg/L, is as effective as increasing the total hardness to 300 mg/L. Criteria for selecting reuse hatchery sites or establishing operating conditions should specify a total water hardness of at least 100 mg/L, a pH of 7 or above, or Cl^- and Ca^{++} levels

equivalent to at least 25 mg/L $CaCl_2$ to control nitrite toxicity problems.

For chronic exposure in soft, low-chloride water, up to 0.030 mg/L NO_2-N causes only a mild methemoglobinemia, no gill pathological changes, mortalities, or growth reduction in freshwater, and no mortalities or growth reduction after smoltification and adaptation to 30‰ seawater. Chronic exposure to 0.060 mg/L NO_2-N causes minimal gill epithelial changes but also had no adverse effects on survival or growth in either freshwater or salt water.

Acknowledgments

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Myxosoma cerebralis: Fluorescent Antibody Techniques for Antigen Recognition

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MARKIW, M. E., AND K. WOLF. 1978. *Myxosoma cerebralis:* fluorescent antibody techniques for antigen recognition. J. Fish. Res. Board Can. 35: 828–832.

Rabbits were immunized with antigens extracted from mature spores or prespore stages of *Myxosoma cerebralis*, and the resulting antisera and their globulins were used in direct and indirect fluorescent antibody techniques. Both kinds of antisera reacted with homologous spores and with stages of the organism that precede spores. When tested for specificity against spores of 12 other myxosporidans the direct fluorescent antibody technique showed cross-reactivity with only one other and that was a species of *Myxosoma*. The indirect fluorescent antibody technique showed some reactions across generic lines. The antisera have application in studies of the parasite's life cycle and in diagnostics.

Key words: spores, parasites, direct fluorescent antibody techniques, indirect fluorescent antibody techniques, diagnosis, myxosporidans, whirling disease

MARKIW, M. E., AND K. WOLF. 1978. *Myxosoma cerebralis:* fluorescent antibody techniques for antigen recognition. J. Fish. Res. Board Can. 35: 828–832.

Des lapins ont été immunisés par antigènes extraits de spores mûres ou de stades de préspores de *Myxosoma cerebralis*. Les antisérums qui en résultèr et leurs globulines ont été ensuite utilisés dans des techniques d'anticorps fluorescents directes et indirectes. Les deux genres d'antisérums réagissent avec des spores homologues et avec des stades de l'organisme précédant les spores. Lorsque essayée en vue de déterminer la spécificité contre les spores de 12 autres myxosporidies, la technique d'anticorps fluorescents directe montre une réactivité réciproque avec seulement un autre, une espèce de *Myxosoma*. La technique d'anticorps fluorescents indirecte réagit avec certains organismes au-delà des frontières génériques. Les antisérums trouvent une applications dans des études du cycle biologique et dans le diagnostic du parasite.

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THE life cycle of *Myxosoma cerebralis*, cause of salmonid whirling disease, is a challenging puzzle to parasitologists and because it is so poorly understood, one of the more difficult problems of those who are concerned with matters of fish health. *Myxosoma cerebralis* has been known for more than 70 yr, but as is true for all myxosporidans, the greater part of its life cycle is an enigma (Fig. 1). Fundamental properties of myxosporidans are in some dispute; most parasitologists consider them to be protozoans, but others note bilateral symmetry and multinucleation — features found in metazoans. Also, with the exception of the term *spores* for the mature stage in the fish, there is a notable lack of unanimity in terminology used for the morphologically different life stages that are presently recognized.

The fish health specialist can diagnose frank whirling disease from its clinical signs and by finding spores that have the size and shape of *M. cerebralis*. In such cases, spores are abundant and easily found. When the incidence of infection is low or if the intensity is light, spores are not abundant. Therefore, the diagnostician would have a difficult task were it not for several procedures that were developed to release and concentrate spores (Landolt 1973; Markiw and Wolf 1974; O'Grodnick 1975). However, whirling disease has a long incubation and at least 3 mo elapse before spores are formed (Fig. 1). During that time, few persons are qualified to make a critical diagnosis, i.e. a positive identification; and such identifications are presumptive.

Serological–immunological methods are widely used to substantiate diagnoses of bacteriological and virological diseases of fishes and the methods have great potential for being keys to the secrets of the *M. cerebralis* life cycle. In addition, the methods can provide the general fish diagnostician with up-to-date means of identification — methods that augment and in time will replace morphometry. Because serological methods can reveal biological relationships, systematists too can profitably use them.

Pauley (1974) was the first to apply immunological methods to *M. cerebralis*. He sought a way of detecting asymptomatic carriers, and found that spore extracts

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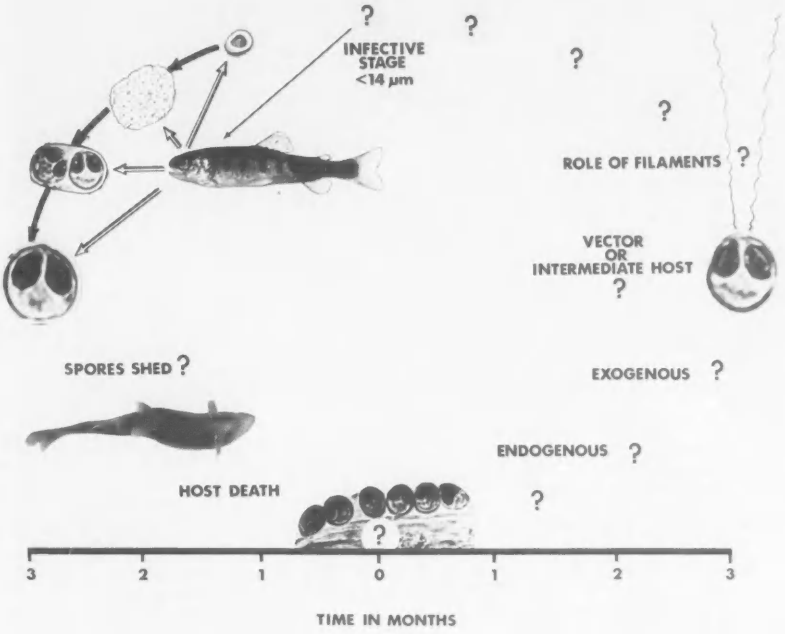

FIG. 1. Schematic life cycle of *Myxosoma cerebralis*. Bicapsular multinucleate spores form in host fish skeletal elements and are assumed to be the mature stage of the organism. Starting at *bottom center*, mature spores enter the environment by host death and decomposition, or defecation by fish-eating predator, or possibly shedding by the host fish itself. Through completely unknown processes requiring at least 3 mo, each spore ultimately gives rise to one or more infective stages. The process may be endogenous or it may involve an intermediate host. The enigmatic coiled filaments within the polar capsules undoubtedly play a crucial role in the life cycle. Virtually nothing is known of the infective stage or of how and where it enters its fish host (*top left*). Several weeks or more after infection, foreign bodies may be found in cartilage and in time give rise to multinucleate stages — whether or not a sexual stage exists is unknown. At a minimum of 3 mo from first infection, sporulation occurs and spores persist for the life of the host. About two thirds of the minimum life cycle is unknown.

were antigenic in rabbits but not in rainbow trout (*Salmo gairdneri*). He presented evidence to show that the parasite's antigens mimicked those of rainbow trout even though the proteins were immunoelectrophoretically different. Halliday (1974) used indirect fluorescent antibody techniques (FAT) and confirmed the reactivity of rabbits to immunization with *M. cerebralis*. However, neither naturally nor experimentally infected rainbow trout showed an immune response, and he concluded that FAT could not be used for diagnosis of whirling disease. Halliday (1974) did find that rabbit antiserum did not react with spores of an unidentified species of *Myxobolus*, and he suggested that serology might be of value in clarifying myxosporidan taxonomy.

The antigenicity of *M. cerebralis* spore extracts in rabbits has been amply demonstrated. We think it likely that some of the parasite's antigens persist throughout all stages of the life cycle, therefore our objective was to ascertain whether fluoresecent antibody techniques would provide specific serological recognition of antigens in spores and in other life stages of *M. cerebralis*.

Materials and Methods

SOURCE AND PREPARATION OF ANTIGENS AND ANTISERA

The method of Markiw and Wolf (1974) was used to release and concentrate spores, as well as prespore stages from experimentally infected rainbow trout. Prespore stages were predominantly ovoid forms, and in unstained wet mounts they showed no obvious internal structures. The method of harvesting spores was modified slightly in that 0.05% (wt/vol) soybean trypsin inhibitor was substituted for bovine serum albumin.

TABLE 1. Summary results of direct and indirect fluorescent antibody tests on spores of 13 myxosporidans reacted with rabbit antiserum against *Myxosoma cerebralis*.

Organism	Test	
	Direct	Indirect
Myxosoma cerebralis	+	+
M. cartilaginis	+	−
M. cephalus	−	+
M. cyprini	−	+
Myxobolus insidiosus	−	+
M. argenteus	−	−
M. sp. (cyprinid)	−	+
Henneguya exilis	−	−
H. zschokkei	−	−
Unicauda sp.	−	+
Ceratomyxa shasta	−	−
Unidentified (salmonid)	−	+
Unidentified (catostomid)	−	+

We used the method of Pauley (1974) to extract soluble antigens from two different preparations — the first being 3.1×10^7 mature spores from adult fish, and the second 4.6×10^7 prespore stages from fingerling fish.

Antigens from each preparation were brought to 3 mL and protein determined by the Folin phenol method of Lowry et al. (1951). The protein content of antigens from mature spores was 1.8 mg/mL and that of prespore stages was 4.2 mg/mL. For immunization, a mixture of 1 mL antigen, 1 mL Freund's incomplete adjuvant, and 2 mL Hanks' balanced salt solution (BSS) was homogenized.

Normal serum was taken from New Zealand white rabbits before they were immunized with intramuscular injections of 0.8 mL antigen homogenate in each hind leg. The inoculum was equivalent to 4.12×10^6 spores each for two rabbits immunized with the mature spore extract and 6.13×10^6 prespore stages for two immunized with the prespore antigen extract. After 12 d the rabbits were bled and their sera separated, distributed in 5-mL subsamples, and lyophilized. For use, the sera were reconstituted with water and diluted with equal volumes of pH 7.0 buffered NaCl (NaCl 8 g, $NaH_2PO_4 \cdot H_2O$ 1.38 g, and NaOH 0.333 g dissolved in 1 L). Sera were then adsorbed with acetone-dried powders of cartilage–bone and liver tissues from healthy adult rainbow trout. Two adsorptions were made at 10°C; the first was static for 1 h and the second continually mixed for 16 h. Tissue powders were used at the rate of 50 mg of each per millilitre of diluted serum, and they were removed by centrifugation for 30 min at 48 200 × *g* at 5°C.

Sera or their precipitated globulins or both from 10 normal rabbits — preinoculation serum from the 4 immunized rabbits and individual sera from 6 others — were tested for suitability as negative controls. We also tested two lots of pooled normal rabbit serum.

Globulins were precipitated at 0°C with ammonium sulfate at 50% saturation washed twice in ammonium sulfate at 60% saturation, reconstituted with 0.05 M potassium–sodium phosphate buffer at pH 7.3 to the original serum volume and extensively dialyzed against 0.002 M potassium–sodium phosphate buffer at 4°C.

For direct FAT we conjugated whole normal rabbit serum, serum globulins, or antisera against *M. cerebralis* with FITC on diatomaceous earth (Celite®, Calbiochem, San Diego, Calif.) according to the method of Rinderknecht (1962). For the indirect FAT we used FITC conjugated with IgG fraction goat antirabbit serum at a dilution of 1:25 in conjunction with a 1:10 dilution of rhodamine conjugated bovine albumin (Cappel Laboratories, Downington, Pa.).

TESTING MYXOSPORIDANS FOR FLUORESCENT ANTIBODY REACTION

In addition to the homologous organism, formalin-fixed spores (the only life stage realistically available) from 12 other myxosporidans were tested for reactivity with both the direct and indirect FAT (Table 1).

For both the direct and the indirect FAT, spores were attached to microscope slides lightly coated with either 50% egg albumin (vol/vol) or Tissue Bond® (Harleco, Gibbstown, N.J.). Slides were dried 15–20 min at 50–60°C, and fixed 5–10 min in methanol. Serum, serum conjugate, or globulin conjugate was tested at dilutions of 1:10, 1:20, 1:40, 1:80, and 1:160. Each dilution was used at 0.1 mL, which was spread over slides for 30–60 min in a darkened humidified container at 20–25°C.

Slides for direct FAT were then washed for 10–15 min in freshly prepared 0.5 M sodium carbonate–bicarbonate buffer (pH 9.0–9.5), blotted dry, covered with low fluorescence immersion oil, and examined microscopically.

For indirect FAT, slides were washed for 10–15 min in pH 7.0 buffered NaCl and blotted dry. Diluted fluorescein conjugated IgG goat antirabbit serum, mixed with rhodamine conjugated bovine albumin, was applied for 30 min in the light-proof humidified chamber at 20–25°C. Slides were then washed with freshly prepared 0.5 M sodium carbonate–bicarbonate buffer as in the *direct method*, blotted dry, and examined as in the direct method.

Slides were coded and a single blind method of scoring was used throughout the work.

Results

Used in either the direct or the indirect FAT, both kinds of rabbit antisera implemented serological recognition of antigens of mature spores and of earlier life stages of *M. cerebralis* (Fig. 2). The direct method, however, was the more specific for with it the only other reactive myxosporidan spores were those of *M. cartilaginis* (Table 1). Conjugates prepared from spore or prespore antiserum or their globulins produced equally fluorescent spores of *M. cerebralis* and *M. cartilaginis*, and the reaction was blocked by unconjugated globulin.

With the direct method maximum brightness of spores was found at dilutions of 1:20 and 1:40, and polar capsules were typically apparent as unstained voids against a fluorescent background that included the sporoplasm and intercapsular substance (Fig. 2). Some spores of *M. cerebralis* were immature — in others the valves or polar capsules were evidently open and in such the developing polar capsules or the polar filaments were also fluorescent. We found no such reactivity in *M. cartilaginis*, but the only spores we had were fully mature.

The two kinds of antisera differed in the intensity of their reaction on *M. cerebralis*. Although measurements were not practical, the oval prespore stages seemed to

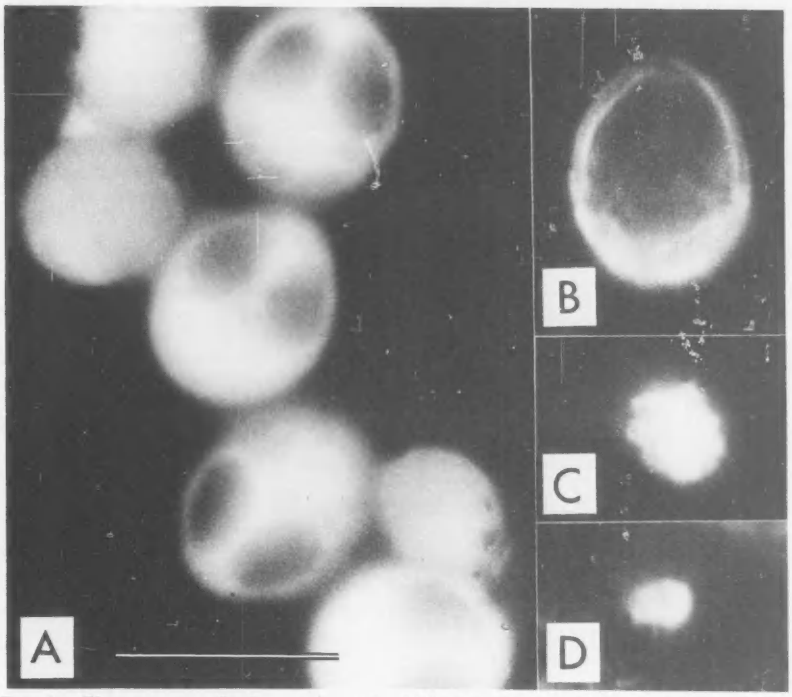

FIG. 2. Fluorescent antibody reactions of rabbit antiserum with *M. cerebralis*. A, Mixed spores and prespore stages (smaller ovals) stained with the direct method. Note the unreactive polar capsules; B, a mature spore stained with the indirect method shows halo-like surface fluorescence; C, 40-d-old form presumptively identified by its reactivity with antiserum in the direct method; D, 2-d-old form in rainbow trout head presumptively identified by the direct method. Bar scale is 10 μm.

stain more brightly with prespore antiserum and fully mature spores with spore antiserum. When two lots of pooled normal rabbit serum or their precipitated globulins were conjugated with FITC, both reacted with *M. cerebralis* to give a false positive fluorescence. We found it necessary to conjugate and test precipitated globulins from individual rabbits to find negative normal serum for the direct FAT. Only two of six rabbits so tested proved suitable and we have no explanation for the unexpected reaction.

With the indirect method, reactivity of *M. cerebralis* occurred at all dilutions of antiserum, but optimum brilliance was obtained at 1:40. The fluorescence of indirectly stained life stages was at the surface, giving a halo-like effect in which polar capsules were not readily apparent (Fig. 2).

With the indirect FAT, 7 of 12 other myxosporidans showed surface fluorescence (Table 1). The fluorescence of heterologous spores was variable from species to species; it was seldom entire and tended toward concentration at the distal end. In *Unicauda* sp. the condition was extreme; fluorescence was confined to the most distal portion of the caudal appendage. Neither *Ceratomyxa shasta* nor the two species of *Henneguya* fluoresced.

With the indirect method, neither *M. cerebralis* nor any other myxosporidan showed fluorescence with normal rabbit serum.

The two methods of fluorescent staining worked with either fresh or preserved spores.

Discussion

The common denominator in our tests of 13 different myxosporidans for FAT reactivity with rabbit anti-*M. cerebralis* serum was the spore stage. Our results leave no doubt that of the two techniques, the direct method was by far the more specific, and this agrees with serological tenets. The FITC conjugated *M. cerebralis* antisera, or their globulins, reacted with homologous spores and with spores of *M. cartilaginis* but not with spores of the other two species of *Myxosoma*. These results suggest a close relationship between the two reactive species, and they also suggest that *M. cephalus* and *M. cyprini* have quite different antigens and may not belong to the genus *Myxosoma*. These findings lend

support to Halliday's contention that serology could clarify myxosporidan taxonomy. We believe serology can greatly improve classification based solely on morphometry.

In the homologous system, the reactivity or prespore stages with antiserum prepared with spore antigens and vice versa supports our hypothesis that some of the parasite's antigens are present throughout its life cycle. Accordingly, while we are not yet prepared to describe them by light microscopy, we believe that the kinds of fluorescent forms illustrated in Fig. 2C and D may be stages of the life cycle.

We recognize that selective purification of *M. cerebralis* antigens will probably be required to provide antisera that will give absolutely specific serological identification. In the meantime, the direct FAT should be used in diagnostic work for it lends added credence to morphometric methods of spore identification. Perhaps most importantly, the direct FAT provides the best available means of identifying life forms of *M. cerebralis* prior to sporulation, and thus extends to many persons the expertise currently possessed by a very few skilled parasitologists. In monitoring a suspect facility we have used the direct FAT to identify an incipient outbreak of whirling disease 2 mo before its actual occurrence.

Members of the genera *Myxosoma* and *Myxobolus* have spores of similar size and shape, and both occur in salmonids. The two are presently distinguished by demonstration of an iodinophilus vacuole in *Myxobolus*, but that test is not reliable with preserved spores. Halliday (1974) found that one unspeciated member of the genus *Myxobolus* did not react to an indirect FAT with *M. cerebralis* antiserum. We found that with the indirect FAT two of three *Myxobolus* species and other genera reacted with anti-*M. cerebralis* serum. The location of the fluorescence suggests that the outer mucoid material is reactive. Such reactivity is indicative of a common external antigen or antigens. According to Lom and Hoffman (1971) *M. cerebralis* has a mucous envelope and *M. cartilaginis* does not. That fact may explain why in the indirect FAT, *M. cartilaginis* was not reactive to antiserum against *M. cerebralis*. In this light, the direct FAT may depend upon antigens from within the valves, and that is consistent with the described appearance of fluorescence throughout the spores of the two species of *Myxosoma*. That being the case serologic comparisons of myxosporidans should utilize internal antigens and direct FAT.

Some normal rabbit sera and their precipitated globulins that were conjugated with FITC gave fluorescence with *M. cerebralis* spores. It seems most unlikely that the reactive sera represented prior antigenic experience of the rabbits to the myxosporidan. Rather, we attribute the nonspecificity to vagaries of the rapid conjugation method we employed, or to possible affinity of the spores to unidentified protein of the conjugate. The false positive reaction was not universal among the rabbits tested, but it is a strong reason for testing rabbits and demonstrating them to be negative before immunizing them with antigens of *M. cerebralis*.

Acknowledgments

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Behavior of Age-Specific, Density-Dependent Models and the Northern California Dungeness Crab (*Cancer magister*) Fishery

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BOTSFORD, L. W., AND D. E. WICKHAM. 1978. Behavior of age-specific, density-dependent models and the northern California Dungeness crab (*Cancer magister*) fishery. J. Fish. Res. Board Can. 35: 833–843.

A continuous time and age model which reflects the effect of older age-groups on mortality in young is presented. The conditions under which this model is unstable and the characteristics of solutions under various conditions are examined. Results obtained are related to results obtained by others from stock–recruitment models. Analytical expressions for the period of oscillations, the effect of fishing all age-classes, and the effect of the slope of the stock–recruitment curve at the replacement point support earlier simulation results. The effect on the model of size-selective fishing is shown to be a decrease in the stability of the population in some cases. These results are demonstrated with a model that approximately reflects the Dungeness crab (*Cancer magister*) population in northern California. The cyclic behavior of this population is similar to an unstable mode of the model. Conditions under which this mode arises are derived and potential causes of decreased stability, among which is fishing, are examined.

Key words: fishery, model, stability, Dungeness crab, age-specific, density-dependent, stock–recruitment, cannibalism, *Carcinonemertes*

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Les auteurs présentent un modèle continu de temps et d'âge reflétant l'effet des groupes d'âge plus âgés sur la mortalité des jeunes. Ils examinent les conditions dans lesquelles ce modèle est instable et les caractéristiques des solutions applicables à diverses conditions. Ils comparent leurs résultats avec ceux obtenus par d'autres à partir de modèles de stock–recrutement. Les expressions analytiques de la période d'oscillations, l'effet de la pêche sur toutes les classes d'âge et l'effet de la pente de la courbe stock–recrutement au point de remplacement confirment les résultats de simulations antérieures. On démontre que l'effet sur le modèle d'une pêche sélective quant à la taille est, dans certains cas, une diminution de l'équilibre de la population. On démontre ces résultats en utilisant un modèle qui reflète à peu près la population de dormeurs du Pacifique en Californie septentrionale. Cette population a un comportement cyclique semblable à un mode instable du modèle. Les auteurs en déduisent les conditions dans lesquelles ce mode prend naissance et examinent les causes possibles de diminution de équilibre, entre autres, la pêche.

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MANY fisheries experience a large yearly variation in catch due to a variation in the size of each year-class. In some fisheries and simulations of fish populations these variations appear to be cyclic and are attributed to inter-age-class, density-dependent effects. This type of behavior raises two important questions for fishery biologists: (1) what characteristics of the density-dependent effects are necessary for cyclic fluctuations to occur, and (2) how does fishing affect the cyclic fluctuations?

Ricker (1954) investigated cyclic populations by simulating populations with nonlinear, stock–recruitment relationships. He found that for populations with a single spawning age-class, persistent oscillations occurred only if the slope of the stock–recruitment curve was < -1 at the replacement point. For multiple spawning age-classes, the slope required for persistent oscillations depended on the number of age-classes present and the age of first spawning. For example, one simulated population with multiple spawning age-classes did not exhibit persistent oscillations even with a stock–recruitment curve whose slope was -1 at the replacement point. Although the cycles produced in the simulations were irregular, their "period" was approximately twice the mean age of reproduction. The effect of exploitation on these populations was to decrease the amplitude and period of oscillations and if exploitation intensity was high enough, to completely eliminate persistent oscillations.

Walters (1969), Larkin (1971), Basasibwaki (1972), and others have simulated populations using stock–recruitment relationships similar to Ricker's. However, only Allen and Basasibwaki (1974) have obtained analytical

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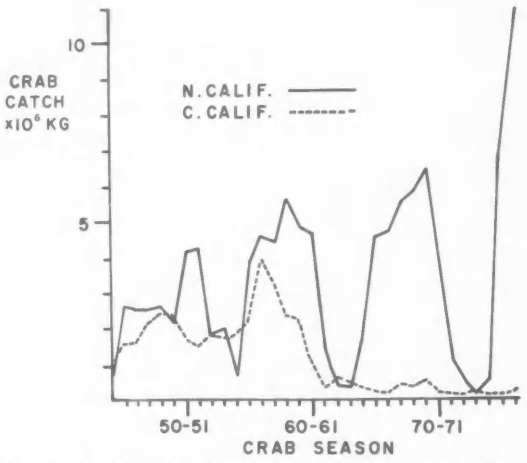

FIG. 1. Total catch of Dungeness crab in northern (Fort Bragg to Crescent City) and central (San Francisco to Bodega Bay) California. Data are from records of the California Department of Fish and Game.

explanations for the generally observed characteristics of cyclic populations. Using a Leslie matrix model (Leslie 1945) coupled to a nonlinear, age-dependent, stock–recruitment relationship they obtained conditions under which persistent oscillations would occur. Menshutkin (1964) examined cyclic fluctuations in a perch population and the effect of fishing by simulating the cannibalistic behavior of individuals directly rather than using a stock–recruitment relationship. Fishing changed the amplitude and period of oscillations, and if intense enough, eliminated them.

Demographers concerned with human populations have recently obtained results pertinent to oscillations in fish populations. Keyfitz (1972) analyzed cycles occurring in populations described by the linear renewal equation (i.e. a constant maternity function) and formulated a simple model of compensatory dependence of birth rate on past birth rates. For the latter, he obtained conditions under which oscillations with period of twice the mean generation time would occur. Frauenthal (1975) analyzed a renewal equation model in which fucundity depended on cohort size. Lee (1974) analyzed two discrete versions of the renewal equation; one in which fertility depended on cohort size and one in which it depended on the size of the labor force. Both obtained conditions for oscillations whose period was twice the mean age of reproduction.

The Dungeness crab (*Cancer magister* Dana) is extensively fished along the Pacific coast of North America. The California fishery is regulated to maintain a high reproductive capacity by allowing only males of carapace width >160 mm to be legally taken. The males have generally had a minimum of 2 yr for reproduction before entering the fishery. Females, although sometimes captured, are not retained. From the high percentage of inseminated females generally found, Poole and Gotshall (1965) concluded that a sufficient number of males were always present for reproduction.

Fluctuations in crab catch appear to be of a cyclic nature, particularly in northern California (Fig. 1). Cleaver (1949) found that recovery of marked adult crabs through the fishery was very high and concluded that virtually all available legal-size crabs were caught each year. This conclusion is supported by the fact that yearly effort (in terms of landings) and catch per unit effort (pounds per landing) vary with the same pattern as catch (data in Anon 1976). Since catching all legal crabs each year implies there is no lag between abundance and effort, the observed cycles do not seem to be caused by a predator–prey cycle with man as the predator.

Peterson (1973) suggested that these cyclic fluctuations followed cycles in the yearly intensity of upwelling. Botsford and Wickham (1975) showed that while upwelling intensity was positively correlated with crab catch, upwelling itself did not appear to be a cyclic process, whereas crab abundance did. The indicated period of the catch cycles was slightly greater than twice the mean age of reproduction. Winnor (1966) and Mayer (1973) noted an inverse relationship between spawning stock and recruitment of their offspring into the fishery 4 yr later. They suggested density-dependent, interage mechanisms such as cannibalism as the cause.

We analyze here a continuous time model similar to the model of Allen and Basasibwaki (1974) and a model with constant reproduction. These models include age-specific, density-dependent mortality in the youngest age-class. The results obtained are related to simulation results obtained by Ricker (1954) and others. The analytical techniques are applied to a preliminary model of the Dungeness crab population to determine whether the current method of fishing can possibly be involved in the generation of existing cycles.

The Model

The model describes recruitment as the product of the rate of reproduction and a survival function which depends nonlinearly on the number in the population

$$R(t) = B(t)\, f[C(t)], \quad 0 \le f[C(t)] \le 1, \tag{1}$$

where $R(t)$ = rate of recruitment; $B(t)$ = rate of reproduction; $f[C(t)]$ = fraction surviving to recruitment; $C(t)$ = the effective size of the population as it affects density–dependent mortality.

In this model the rate of reproduction, $B(t)$, is considered to be the rate at which individuals of age 0 appear. The fraction of these surviving to an age >0 is $f[C(t)]$ which depends on $C(t)$, a weighted integral over all ages >0. Recruitment $R(t)$ is then the rate at which animals of age >0 appear. The point in an individual's life history that is considered to be age 0 depends on the specific density-dependent mechanism being modeled. Figure 2 is an example in which age 0 is the point at which individuals leave the larval phase. Modeling the occurrence of density-dependent mortality at a single age is an

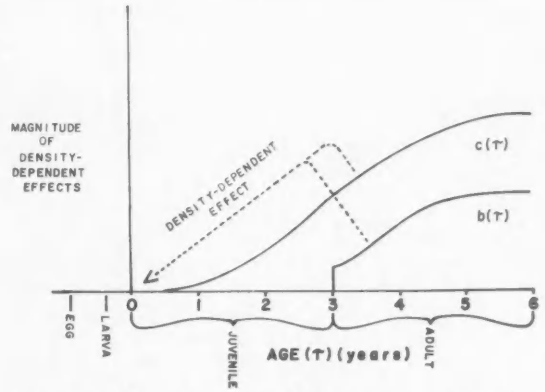

FIG. 2. A schematic example of the elements of the model. Age 0 is taken to be the time of metamorphosis from the larval stage. The relative effects of older animals through reproduction and density-dependent mortality on the number at age 0 are indicated by functions $b(\tau)$ and $c(\tau)$, respectively. These functions indicate the effect per number present at each age.

approximation made to provide a mathematically tractable problem. As long as the actual occurrence is over a small time period near age 0 no significant error is incurred.

We consider two different expressions for the rate of reproduction, $B(t)$. For some populations, the rate of reproduction depends on the number of mature individuals present and the fecundity at their age. To simplify the analysis we assume for the present that we are concerned only with females (this assumption is modified in the application to the Dungeness crab population)

$$B(t) = \int_0^\infty n(a, t)b(a)da, \tag{2a}$$

where $n(a, t)da$ = number of individuals of age a at time t, and $b(a)$ = number of offspring per individual of age a.

For some marine organisms, the number of young surviving the larval phase is considered to be independent of the size of the adult population as long as the reproductive capacity of the population is greater than a certain minimum value. This is based on the assumption that the pelagic environment of the larvae has a limited "carrying capacity" which is exceeded each year by the high fecundity of the adult population. Whether or not this is the case for the Dungeness crab is unknown; however, if it were the case, reproduction in the model would be constant and unaffected by the distribution of mature females over age. To investigate this possibility, the effects of a second expression for reproduction are examined. If reproductive level is a constant (B_c) the alternative expression to (2a) is

$$B(t) = B_c. \tag{2b}$$

The effect of the population on recruitment mortality depends on the number present and the relative contribution at each age.

$$C(t) = \int_0^\infty n(a, t)c(a)\,da, \tag{3}$$

where $c(a)$ = the relative influence of an individual of age a on recruitment mortality.

Since mortality for age >0 is a function of age only (i.e. does not depend on time or density), the number of individuals of age a at time t is the product of the number present at age 0 and time $t - a$, and the survival to age a.

$$n(a, t) = n(0, t - a)\sigma(a), \tag{4}$$

where $\sigma(a)$ = the fraction surviving to age a from age 0. Since $R(t - a)$ is equal to $n(0, t - a)$, we can rewrite (2a) as

$$B(t) = \int_0^t R(t - a)\sigma(a)\,b(a)\,da + G_B(t), \tag{5}$$

where $G_B(t)$ = reproduction from individuals present at time $t = 0$, and (3) as

$$C(t) = \int_0^t R(t - a)\sigma(a)c(a)\,da + G_C(t), \tag{6}$$

where $G_C(t)$ = density-dependent mortality effects due to individuals present at $t = 0$. We assume that $\sigma(a)c(a)$ and $\sigma(a)b(a)$ are zero for $a > \alpha$, and that we are concerned only with time $t > \alpha$, hence $G_B = G_C = 0$.

Equilibrium and Linearization

As time increases, recruitment may approach an equilibrium value. To determine the equilibrium value of $R(t)$, R_e, we let time, t, go to infinity to reflect recruitment reaching equilibrium after a relatively long time and replace $R(t - a)$ with R_e in (1), (5), and (6). For reproduction given by equation (2a)

$$R_e = f^{-1}\left(\frac{1}{\Phi_b}\right)\frac{1}{\Phi_c} \tag{7a}$$

and for constant reproduction (equation 2b)

$$R_e = B_c f[R_e\Phi_c], \tag{7b}$$

where we have defined influence functions (functions describing the influence of older age-classes on individuals of age 0), ϕ_b and ϕ_c, and their integral over all age, Φ_b and Φ_c, to be

$$\Phi_b \equiv \int_0^\infty \phi_b(a)\,da; \quad \phi_b(a) \equiv b(a)\sigma(a); \tag{8}$$

$$\Phi_c \equiv \int_0^\infty \phi_c(a)\,da; \quad \phi_c(a) \equiv c(a)\sigma(a). \tag{9}$$

We assume that solutions to (7a) and (7b) exist and, therefore, that at least one equilibrium state exists for each model. These solutions depend on the function $f[C(t)]$ used to represent the interage mechanism present in a specific population. For a population that appears to vary about an equilibrium value a solution should exist if the model adequately reflects the dynamics of the population.

To determine local stability about the equilibrium point we use a linear approximation of the model. We

define $\delta R(t) \equiv R(t) - R_e$ to be a small deviation from equilibrium recruitment. From

$$\text{(10a)}\quad \delta R(t) = \int_0^t \delta R(t-a)\phi_b(a)\,da\, f[R_e\Phi_e] + f'[R_e\Phi_e]\int_0^t \delta R(t-a)\phi_c(a)\,da\, R_e\Phi_b$$

and the appropriate equilibrium condition we obtain

$$\text{(10b)}\quad \delta R(t) = \int_0^t [\tilde{\phi}_b(a) + K\tilde{\phi}_c(a)]\,\delta R(t-a)\,da$$

for reproduction given by (2a) and the same expression with $\tilde{\phi}_b$ absent for constant reproduction. In both cases

$$K = \frac{R_e\Phi_c f'(R_e\Phi_c)}{f(R_e\Phi_e)};\quad f'(x) = \frac{df(x)}{dx};$$

and normalized ϕ functions are defined

$$\tilde{\phi}_b(a) \equiv \frac{\phi_b(a)}{\Phi_b(a)};\quad \tilde{\phi}_c(a) \equiv \frac{\phi_c(a)}{\Phi_c(a)}.$$

Since f reflects compensatory mortality, f' (and therefore K) will in the most common situation be negative at equilibrium. Equation (10b) can be interpreted as indicating that the current value of the deviation from equilibrium recruitment depends on a weighted sum of past values of the deviation from equilibrium recruitment. Each past value is weighted by the reproductive influence function (ϕ_b) at the appropriate age, and K times the density-dependent influence function (ϕ_c) at the appropriate age. The parameter K can be interpreted as a "normalized" derivative of the survival function, f, at equilibrium.

Stability

Since equation (10) is a linear equation, solutions will be of the form

$$\text{(11)}\quad \delta R(t) = \sum_{i=1}^{\infty} q_i\, e^{r_i t},$$

where q_i's are real constants and r_i's are complex roots of the equation

$$\text{(12)}\quad \int_0^{\infty} e^{-t\tau}[\tilde{\phi}_b(\tau) + K\tilde{\phi}_c(\tau)]\,d\tau = 1$$

The root with the largest real part will dominate the solution for large time. The system will be locally stable (i.e. $\delta R(t) \to 0$ as $t \to \infty$) if the real part of the dominant root is negative, and locally unstable (i.e. $\delta R(t) \to \infty$ as $t \to \infty$) if it is positive. If the real part of the dominant root is zero, persistent oscillations will occur if the imaginary part is nonzero. A constant level will be maintained if the real and imaginary parts are zero. In general, analytical solutions to (12) are difficult to obtain; however, investigation of some special cases can provide insight into the system behavior. To investigate these special cases we define a total influence function.

$$\text{(13)}\quad \phi(a) \equiv [\tilde{\phi}_b(a) + K\tilde{\phi}_c(a)]$$

and

$$\Phi \equiv \int_0^{\infty} \phi(a)\,da.$$

Stability conditions on K are given for the model of reproduction in (2a) for three special cases, followed by the differences between these and the conditions for constant reproduction (2b). For reproduction given by (2a), $\Phi = 1 + K$. For the case in which reproduction is dominant (i.e. $\tilde{\phi}_b(a) > |K|\tilde{\phi}_c(a)$ for all a), $\phi(a)$ is positive and the solutions are the same as the standard linear renewal equation (Keyfitz 1968). The dominant root is real and the system is stable for $K < 0$, unstable for $K > 0$ and maintains a constant value for $K = 0$. Oscillations can occur but will not dominate the solution. The period of oscillation is approximately equal to the mean age of $\tilde{\phi}(a)$.

For the case in which density-dependent mortality is dominant (i.e. $\phi_b(a) < |K|\phi_c(a)$, for all a), $\phi(a)$ is negative and all of the roots are complex. The dominant root will produce oscillations whose magnitude increases with time if the real part of the dominant root is greater than zero and decreases with time if it is less than zero. By solving (12) for the value of K for which the solution is purely imaginary (defined to be K'), we can determine the level of compensatory mortality above which the system is unstable. This value must be less than minus one (Appendix A). The results of an approximate solution (Appendix A) are that the period of oscillations is twice the mean age of $\phi(a)$, and the value of K that produces persistent oscillations is

$$\text{(14)}\quad K' \simeq -\left[\frac{1}{1 - \frac{v^2\pi^2}{2}} + 1\right],$$

where $v = s/\mu$ and μ and s are the mean age of $\phi(a)$ and "standard deviation" about the mean age $\phi(a)$, respectively (see Appendix A for precise definitions). This result shows approximately how the occurrence of persistent oscillations depends on the shape of the compensatory mortality function, ϕ, as well as its magnitude.

The third case of interest is that in which only older animals of one specific age affect reproduction and density-dependent mortality of young. If we assume that $\phi(a) = (1 + K)\delta(a - a_s)$, where δ is an impulse function and a_s is the age of spawning or influence on mortality of young, the period of oscillation is $2a_s$ and the value of K that produces persistent oscillations is $K' = -2$. For $-2 < K < -1$ damped oscillations occur (stable) and for $K < -2$ oscillations whose magnitude increases with time occur (unstable). For $-1 < K < 0$ a decaying exponential solution is produced, while for $K > 0$ an increasing exponential occurs (Appendix B).

For a model with constant reproduction, $\phi_b(a)$ is absent from (13) and $\Phi = K$. The stability conditions on K are identical in all cases except that the bounds on K are increased by one for each condition and the case in which reproduction is dominant is obviously not relevant for this model. In the single age-class case K replaces $(1 + K)$ in the expression for $\phi(a)$.

In summary, although determination of the local stability characteristics requires a solution to equation (12) for the dominant root, the qualitative nature of the behavior of a specific population can be determined by the relative magnitude of compensatory and depensatory terms and the behavior each tends to produce. The depensatory term tends to produce exponential growth or decay, with possible nondominant cycles of period approximately equal to the mean age of reproduction. The compensatory term tends to produce exponentially growing or decaying cycles of period approximately equal to twice the mean age of the density-dependent effect. For persistent oscillations to occur in the latter case, the "normalized" slope (K) of the density-dependent survival function (f) must be more negative than a parameter K' which depends on the shape of the influence function (ϕ). The value of K' is minus one for the single age-class case and generally decreases as the number of age-classes increases.

Effect of Fishing

The effect of fishing on populations, in most fisheries, is to decrease survival at older ages. This is reflected in the model by an appropriate decrease in the survival function $\sigma(a)$, which in turn decreases the influence functions, $\tilde{\phi}_c$ and $\tilde{\phi}_b$ (equations 8 and 9) at older ages. The effects of this change are twofold: (a) to change the equilibrium point (by changing Φ_b and Φ_c in equation 7), which may change the value of K (equation 10), and (b) to change the age dependence of $\tilde{\phi}_b$ and $\tilde{\phi}_c$ (equation 10), which may change K'(the value above which K must remain for the system to be stable). If a change in either K or K' due to fishing causes K to become less than K', the population becomes unstable. The effect of changing the value of K depends on the shape of the function, f. For example, if $f(C(t))$ is linear in $C(t)$ over a certain range about $f(R_c\Phi_c)$, then a change in $R_c\Phi_c$ due to the fishing will not alter K as long as $f(R_c\Phi_c)$ remains in the linear range.

Although determination of the effect of fishing on stability generally requires solving equation (12) with $\sigma(a)$ changed to reflect the effects of fishing, the effect of constant fishing pressure over all ages can be determined directly. The effect of this type of fishing is to multiply $\sigma(a)$ by a factor e^{-ma}, where m reflects the level of fishing pressure. If a certain value of r is a root of equation (12) without fishing, the effect of fishing on the root is to decrease r by m. Since the real part of the dominant root is decreased, the effect of the changes in influence functions, $\tilde{\phi}_b(a)$ and $\tilde{\phi}_c(a)$, is an increase in stability. If fishing does not change the equilibrium point, the actual value of K is not changed, and the system becomes more stable with fishing.

For the case in which density-dependent mortality is dominant, the approximate solution to (12) (equation 14) intuitively demonstrates the effects of fishing. For example, if fishing pressure were applied only to individuals above a certain minimum age, it would in most instances (e.g. when $\phi(a) = 0$; for $a < a_c$, a_c a constant) decrease v (the ratio of "standard deviation" to the mean age of $\phi(a)$). If this were the case and $0 < v < 2/\pi$, the magnitude of K' would decrease. If K did not change, the system would then become less stable due to fishing.

Dungeness Crab

Life-history data on the Dungeness crab are less complete than for many fished populations. Although the population seems to exhibit cycles in abundance of the same nature as those implied by the model, a causal mechanism has not been identified. However, a preliminary model has been constructed for the purposes of (a) providing an example of the analytical characteristics derived earlier and (b) testing the hypothesis that fishing could decrease the stability of a model which at least approximately reflects a real population.

Since in the northern California crab fishery only males above 160 mm carapace width are fished and the influence of males and females on mortality of the young may differ, the model is modified to explicitly include the effects of each sex. The expression for ϕ_c becomes

$$\phi_c(a) = \sigma_m(a)c_m(a) + \sigma_f(a)c_f(a), \tag{15}$$

where σ's and c's are as defined earlier except they apply to a specific sex, with f denoting females and m denoting males. The expression for ϕ_b is

$$\phi_b(a) = \sigma_f(a)b(a), \tag{16}$$

where we assume that the number of mature males is always sufficient to inseminate the entire female population (Poole and Gotshal 1965).

Because the density-dependent mechanisn responsible for cycles in abundance has not been identified, the form of the compensatory influence function, ϕ_c, must be assumed. Two possible mechanisms are cannibalism of young by older crabs and competition for food between young and older crabs. Butler (1954) and Gotshall (1977) showed that young-of-the-year crabs were preyed on by older conspecifics. A third possible density-dependent source of mortality is egg predation by the nemertean worm *Carcinonemertes errantia*, which Wickham (1978) found to be specific to its host, *Cancer magister*. This worm has increased in abundance in northern California over the last 4 yr, apparently in response to the increase in host abundance (D. E. Wickham unpublished data). Since the first two mechanisms may be related to food abundance, we assume that density-dependent mortality depends on the energy requirements of the population. As the total energy requirements of the population increase, the amount of food available decreases, thereby increasing competition or the propensity for cannibalism. Since measurements of the energy requirements of aquatic organisms usually indicate that the energy required for oxidative metabolism is the largest component and is proportional to weight to an exponent near 0.8, the functions $c_f(a)$ and $c_m(a)$ are assumed to be the weight of females and males, respectively, to the 0.8 power.

Since no growth data exist for northern California

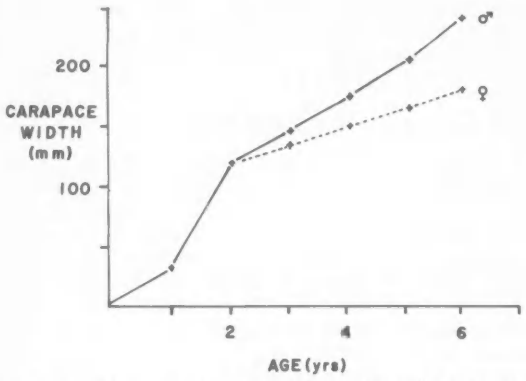

FIG. 3. Estimates of carapace width at each age for male and female Dungeness crab (data from Butler 1961).

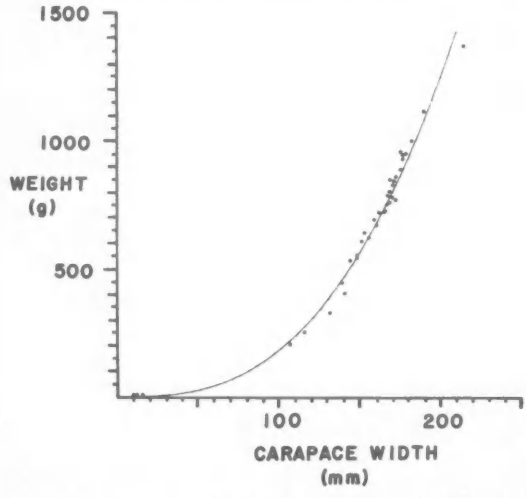

FIG. 4. Weight as a function of carapace width for the Dungeness crab (data from Gotshall and Hardy 1969; D. E. Wickham unpublished data). The line (weight = 0.00055, width 2.76) was obtained by a regression on the logarithm of each variable.

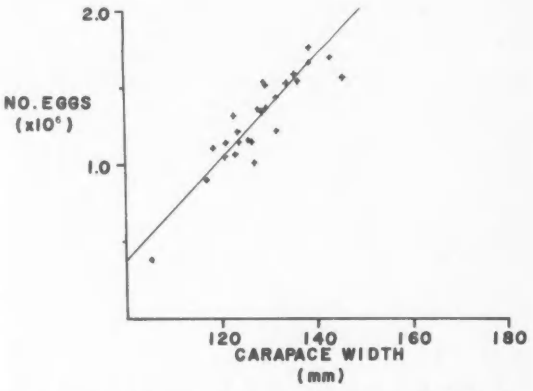

FIG. 5. Fecundity as a function of carapace width for the Dungeness crab (data from Mayer 1973; D. E. Wickham unpublished data).

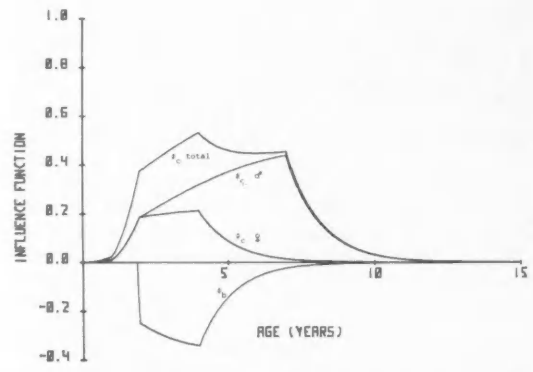

FIG. 6. Male and female components of the influence function, ϕ_c, along with the total influence functions, ϕ_c and ϕ_b. The functions ϕ_c and ϕ_b are shown as opposite in sign to reflect compensatory mortality.

populations, growth in the model was based on data from British Columbia (Butler 1961). Butler's data are similar to those of Cleaver (1949) for Washington and MacKay and Weymouth (1935) for British Columbia. Values of carapace width (measured just anterior to the lateral spine) for various crab instars and estimates of the age of each instar are shown in Fig. 3 (Butler 1961).

The relationship between weight and carapace width was used to convert growth in carapace width to weight. Measurements taken in our laboratory and data from Gotshall and Hardy (1969) are shown in Fig. 4 along with the computed regression. Mayer (1973) measured fecundity as a function of size. His data and the computed regression are shown in Fig. 5.

Data on mortality of mature crabs are sparse. Tagging studies by Cleaver (1949) and Jow (1965) showed very high rates of return and indicate that the predominant source of mortality in mature crabs is removal by the fishery. Jow (1965) estimated natural mortality to be 0.15/yr from his tag–release study using male legal size crabs. Because natural mortality is poorly known, several different mortality functions were examined. The general form was a constant mortality rate of 0.2/yr up to a point of senescence at which it was increased to 0.9. Due to differences in size and reproductive role, mortality functions may differ between sexes. The point of senescence was varied over 4–7 yr for each sex.

The complete, hypothetical model is shown in Fig. 6 as the female and male components of ϕ_b and ϕ_c with the points of senescence taken to be 4 yr for females and 7 yr for males and mortality rate of 0.2/yr up to that point. The reproductive and density-dependent functions

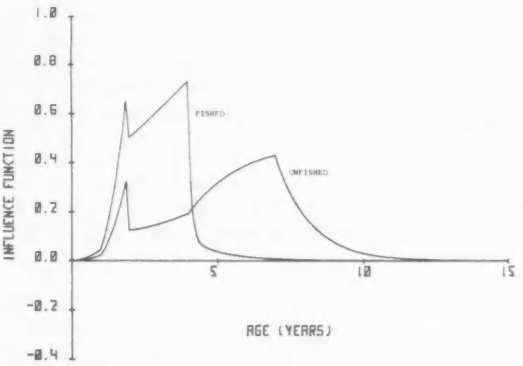

FIG. 7. Total influence function (ϕ) for fished and unfished populations with reproduction given by equation (2a).

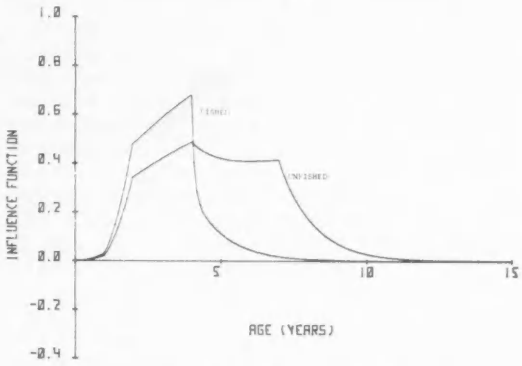

FIG. 8. Total influence function (ϕ) for fished and unfished populations with constant reproductive level (equation 2b).

are shown with opposite signs reflecting a negative value of K.

Results

The basic approach to analysis was to determine the stability of the population with and without fishing. The value of K and the imaginary part of the root for which the real part was zero were determined under both conditions. As stated earlier, this yields the value of K below which the population will display oscillations of increasing magnitude and the period of persistent oscillations. In addition to changing the value of K required for increasing oscillations (i.e. K'), fishing can, in general, change the actual value of K by altering Φ_b and Φ_e and R_e. Since females are not fished, Φ_b does not change in this situation. Since density-dependent mortality was assumed to depend on food abundance, $R_e\Phi_e$ was assumed to be unchanged by fishing (i.e. a population of the same "metabolic size" can be maintained, although its age structure will change).

For the model in Fig. 6 with reproduction expressed by (2a), fishing increased the value of K' and decreased the period of dominant oscillations (Table 1). For the model with reproduction expressed by (2b), the value of K' increased and the period of dominant oscillations decreased with fishing. In each case the period of oscillations was reduced and the value of K required for an unstable solution was increased by fishing. Thus, if the actual value of K were between the value of K' for fished and unfished populations, a stable population would be made unstable by fishing. The effect of fishing on the influence functions (ϕ) can be seen in Fig. 7 and 8.

TABLE 1. The values of K' (top number) and the period of oscillations (bottom number) for fished and unfished populations with reproduction assumed constant and reproduction by a fecundity function, for various parameter values.

Condition	Reproduction by equation (2a)		Reproduction by equation (2b)	
	Unfished	Fished	Unfished	Fished
Baseline: mortality rate 0.2 up to 4 yr (♀) and 7 yr (♂)	−3.0 11.25	−2.75 5.75	−2.75 9.50	−1.75 6.25
Point of senescence changed to 5 yr (♀) and 7 yr (♂)	−3.25 10.75	−3.0 6.0	−2.5 9.5	−2.25 6.5
Point of senescence changed to 5 yr (♀) and 5 yr (♂)	−3.25 8.0	−3.0 6.0	−2.25 8.0	−2.25 6.5
Point of senescence changed to 7 yr (♀) and 5 yr (♂)	−3.5 8.5	−4.25 5.75	−2.5 8.75	−4.0 6.0
Point of senescence changed to 7 yr (♀) and 7 yr (♂)	−3.25 10.5	−4.25 5.75	−2.25 10.25	−4.0 6.0
Mortality rate below senescence changed to 0.15	−2.75 12.25	−2.75 5.75	−2.5 10.0	−1.75 6.25
Total ϕ_e lagged 1 yr			−2.0 11.5	−1.25 8.25

To determine the sensitivity of these results to assumptions made concerning natural mortality, the values of K' and period were computed for several different parameter values. As seen in Table 1, not all variations of the model were made less stable by fishing. For the various parameter values the approximate solution for K' (equation 14) did not always yield an accurate estimate of K' but did change in the correct direction with fishing.

Discussion

The results obtained here provide an analytical basis for the behavior of simulations observed by Ricker (1954). For the single age-class case, $1 + K$ (or alternatively K for constant reproduction) corresponds directly to the slope of the stock–recruitment curve; the results can be directly compared and are identical. Ricker's results for multiple age-classes are a special case of the analytical results obtained here. In his simulations recruitment was a nonlinear function of a weighted sum of reproductive individuals, whereas in the model used here recruitment depends not only on a weighted sum of reproductive individuals, but also on a survival factor which in turn depends on a different weighted sum of

individuals in the population. Because of the additional complexity, direct comparison of results is not possible in all cases. However, in general, the results obtained by Ricker using the reproductive weighting function hold true for total weighting function (equation 13). We have shown that the quantity that corresponds to the slope of the stock–recruitment curve must be < -1 for oscillations to occur. The value required for oscillation can be estimated from equation (14) or solved for exactly with the method employed in the Dungeness crab example. In the approximation of equation (14) and in numerical solution, its value decreased as the ratio of standard deviation to the mean of the influence function (ϕ) decreased.

The "period" of oscillations in Ricker's simulations was always twice the mean age of reproduction. More generally the period of dominant oscillations is twice the mean age of the total influence function which includes reproductive as well as density-dependent effects (for $\phi(a) < 0$, Appendix A). Ricker's result follows from his use of the reproductive weighting function in all simulations.

The results obtained by Allen and Basasibwaki (1974) can be compared directly, since their model is a discrete time, discrete age analog to the model used here with reproduction given by (2a). The results obtained here can also be obtained with that type of model. (Keyfitz (1968) discusses the relationship between the discrete and continuous models.) For conditions that are equivalent to $\phi(a) > 0$, they derive requirements for stability that correspond to the conditions on K following equation (13). For conditions that correspond to $\phi(a) < 0$, and $\phi_c(a) = \phi_b(a)$, they derive requirements for stability that correspond to a special case of the requirement $K' < -1$ (Appendix A).

Our results differ from Ricker's (1954) simulations and from the simulations and solutions for dominant roots of Allen and Basasibwaki (1974) in that the effect of fishing is not always an increase in stability. Their results are obtained with equal fishing pressure applied to all age-classes and are supported by analytical results obtained here. However, as shown in the Dungeness crab example, selective fishing of older age-classes can actually decrease stability. The effect of fishing on stability depends not only on the change in shape of the influence function, ϕ (which changes the value of K required for stability, K'), but also the effect of fishing on the actual value of K through a change in the equilibrium level. The change in equilibrium caused by changes in Φ_c and Φ_b (equations 7a and 7b) can change the value of K. Ricker (1954) also noted a change in equilibrium level with fishing in his simulations.

The changes in K' due to fishing follow a general pattern in that if the approximate ratio of width to mean of the influence function (ϕ) is decreased by fishing, then K' increases, whereas if the width of the influence function is not greatly changed by fishing, K' decreases or is constant. This general pattern supports the implications of equation (14) and can be seen in Table 1. As the point of senescence in females increases, the population is less susceptible to an increase in K' due to fishing, since females are not fished. However, as the point of male senescence increases, the population is more susceptible to an increase in K' due to fishing, because the relative width of the influence function is decreased by fishing. Based on this pattern it seems that populations in which females are fished in addition to males would be more susceptible to an increase in K' due to fishing. Also, the effect of possible female mortality due to catching females in the traps, raising them to the surface, then releasing them may be significant in the crab fishery and would tend to increase K'.

The exact way in which K changes due to fishing depends on the specific biological nature of density-dependent mortality. In the crab example, this mortality depended on food level only and did not change with fishing. Based on similar reasoning one would expect similar behavior for other "resource dependent," density-dependent mechanisms. For reproduction given by equation (2a), if females are not fished, Φ_b, and therefore K, remain constant. However, for reproduction given by equation (2b) a change in Φ_c can change R_e and hence K. For density-dependent mechanisms that are not "resource dependent" (e.g. the propensity to cannibalize is independant of the amount of available food), fishing will lead to a change in the value of K.

The model with reproduction given by (2a) is inherently more stable than the alternative model with constant reproductive level. The expressions for K are equivalent (i.e. $R_e\Phi_b$ in one corresponds to B_e in the other), and K' for the constant reproduction model is always less than for the alternative model. The greater inherent stability is due to the depensatory term, ϕ_b, in the influence function, ϕ, which must be overcome by the compensatory effect of ϕ_c. The model with reproduction given by (2a) is also less susceptible to destabilization due to fishing because females are not removed by the type of fishing described; hence, the depensatory influence is maintained.

Results obtained here are directly pertinent to local stability about an equilibrium point. Some of the more global aspects of stability are touched upon in our consideration of how the equilibrium point changes with fishing and how this change affects local stability. However, we have not investigated here the existence of other isolated equilibrium points, nor have we examined the behavior of the model for large excursions from equilibrium during which one of these other equilibrium points could be approached.

The specific results for the hypothetical crab population model demonstrate the possibility of fishing causing an unstable population. Whether or not the Dungeness crab population was rendered unstable by fishing requires field data to confirm whether or not K lies between the fished and unfished values of K'. The solution resulting from an unstable mode of the model, an oscillation of exponentially increasing magnitude approximates the actual catch record (Fig. 1). The values obtained for the period of cycles with fishing are lower than the observed period. A possible explanation is the fact that the time lag between the time that a population achieves a certain metabolic

size and the time that the food supply (and hence degree of cannibalism) reflects this size has been omitted. To investigate the effect of including this lag, the values of K' and the period were computed with $c(t)$ shifted by 1 yr in the positive age direction. For reproduction specified by (2b), the value of K' changed from -2 to -1.25 and the period changed from 11.5 to 8.25 with fishing. The fact that this case in which the width of ϕ_c is reduced not only by fishing but by introducing a lag leads to the highest value of K' observed in all trials supports the implications of equation (14).

One of the benefits of a theoretical modeling study, conducted before definitive data are available, is insight into the type of data that is most important and what numerical values they must have for certain theoretically derived results to be applicable. For the Dungeness crab application a definite hypothesis to be tested in the field is difficult to obtain because of the wide variety of potential, density-dependent mechanisms. However, we can place some requirements on the observed behavior in the field which are theoretically necessary for instability. For the influence function used here the value of K' in the baseline case with fishing and constant reproduction was 2.25. This implies a unit change of $C(t)$ must produce a change in survival of 2.25 units, near equilibrium (the units in each case are the equilibrium values). Identification of a mechanism causing an unstable population requires field data on the change in mortality as the density ($C(t)$) changes.

Cannibalism has been observed in a variety of species and is not necessarily an aberrant behavior confined to conditions of stress (e.g. starvation, high density), but may serve as means of regulating abundance in response to limited resources (Fox 1975). The effect of this behavior is to maintain a small population of "healthy" (e.g. well fed) individuals rather than a larger population of "unhealthy" individuals. Fox (1975) reviews feeding rates of cannibalistic predators, which vary from 0 to 40% of total food and the resulting mortality of cannibalized prey, which can be as high as 95% of an age-class.

Field studies of the relationship between cannibalistic feeding level and prey mortality are necessary to rigorously implicate this mechanism in cycles of abundance. Gotshall (1977) found that young crabs constituted 7.1% of the food items in a survey of Dungeness crab in Humboldt Bay. Butler (1954) found young crabs to be 25 and 8% of the food items in two age-classes of Dungeness crabs in the Queen Charlotte Islands region of British Columbia. Determination of prey mortality rates of young crabs requires further study of other factors, such as larval mortality.

Other forms of intraspecific competition could provide a mechanism for the observed behavior. Competition for food in which older individuals had the advantage over younger organisms is one example. A second example for which some data exist concerns a nemertean worm that preys and reproduces on crab eggs. In a limited sample (4 yr), the number of worms per female increased with the size of the population (D. E. Wickham unpublished data). Thus, egg mortality rate may increase as the number of reproductive females increases. In a model of this phenomenon, the expression of reproduction by equation (2b) is irrelevant and the function $c(t)$ would be the maternity function $b(t - t_1)$ with a lag t_1 that reflects the time from egg laying to predatory behavior in the life cycle of the worm. This mechanism is similar to one proposed for the Adams River sockeye salmon (Larkin 1971) in that the size of the predator population is proportional to the size of the prey population at an earlier time.

The advantages of the age-specific models used here over standard stock–recruitment models are that they allow density-dependent relationships to be based on the specific behavior of individuals in the population and include the dynamics of age structure. Although stock–recruitment relationships are sometimes derived from individual behavior (Harris 1975), the dynamics of age structure are not included in further analysis. Analysis of explicit effects of changes in equilibrium level, the density-dependent effects and age structure are a step toward more realism in fishery models.

Although adequate data are not available to completely define the mechanism of density dependence in the crab population and we have not proven that fishing has caused the population to be unstable, the foregoing analysis does suggest some potentially disastrous consequences. At least one density-dependent mechanism (cannibalism) has been observed. The observed behavior of the catch record, cycles of increasing magnitude, is the same as that predicted by an unstable mode of the model. If the catch records were projected ahead several years on the basis of the model, the catch would drop below zero. This is obviously unrealistic and beyond the range over which the linear approximation applies. However, whether the model applies exactly or not, an inter-age-class density-dependent mechanism is quite likely responsible for the cycles in abundance.

Catch records for the northern California crab fishery (Fig. 1) indicate an abundance of legal crabs in each of the past 2 yr in excess of any previous year. If a mechanism for suppression of survival of young by older age-classes exists in this population, low levels of abundance would be expected in the next few years. Other fluctuating, exploited populations have declined to low levels from which recovery has been slow or nonexistent. Bell et al. (1977) analyzed oscillations in whitefish catch in Lesser Slave Lake. Although the mechanism implicated in these oscillations was a predator–prey cycle (with fishermen as the predator), this population declined, after a year of high abundance, to a low level from which recovery has been slow. Peterman (1977) demonstrated the theoretical possibility of a population with a compensatory effect of stock on recruitment at high levels, but a depensatory effect at low levels, declining quickly from a very high to a very low, stable level. He noted that this was not inconsistent with commonly observed large recruitment just prior to collapse of fish populations.

These considerations are cause for concern over the possibility of the northern California fishery declining to a low level from which it cannot recover, as did the

central California fishery in the early 1960s. A change in fishery policy may be warranted. Optimal fishery policy for models of this type is currently being investigated.

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Appendix A

From equations (12) and (13), a purely imaginary root must solve

$$\text{(A1)} \qquad \int_0^\infty e^{-r\tau}\,\phi(\tau)\,d\tau = \int_0^\infty e^{-iy\tau}\,\phi(\tau)\,d\tau = 1,$$

where $r = x + iy$ and the real part (x) has been set equal to zero. From the relationship

$$e^{-iy\tau} = \cos(y\tau) - i\sin(y\tau),$$

we obtain for the real part,

$$\text{(A2)} \qquad \int_0^\infty \phi(\tau)\cos(y\tau)\,d\tau = 1,$$

and for the imaginary part,

$$\text{(A3)} \qquad \int_0^\infty \phi(\tau)\sin(y\tau)\,d\tau = 0.$$

A necessary condition for the solution of (A2) is $\Phi \geq 1$. To approximate the period and value of K' we define

$$\mu \equiv \frac{1}{\Phi}\int_0^\infty \tau\phi(\tau)\,d\tau,$$

$$s^2 \equiv \frac{1}{\Phi}\int_0^\infty (\tau - \mu)^2\phi(\tau)\,d\tau.$$

We can approximate the sine and cosine functions by the first several terms of a Taylor's series expansions about $\tau = \mu$.

$$\sin(y\tau) \simeq \sin(y\mu) + y\cos(y\mu)(\tau - \mu),$$

$$\cos(y\tau) \simeq \cos(y\mu) - y\sin(y\mu)(\tau - \mu) - (y^2/2)\cos(y\mu)(\tau - \mu)^2.$$

For the imaginary part

$$\int_0^\infty \phi(\tau)[\sin(y\mu) + y\cos(y\mu) - (y^2/2)\sin(y\mu)(\tau - \mu)^2]\,d\tau = \sin(y\mu)\Phi.$$

Equation (A3) becomes

$$\sin(y\mu)\Phi \sim 0,$$

which implies $y\mu = n\pi$, $n = 0, 1, 2 \ldots$. For $n = 1$, the period of oscillation $T = 2\pi/y = 2\mu$. Since $\cos(\pi) = -1$, the real part is

$$\int_0^\infty \phi(\tau)[-1 + (y^2/2)\cos(y\mu)(\tau - \mu)^2]\,d\tau = -\Phi + (y^2/2)\Phi,$$

and equation (A2) yields

$$1 + K' \simeq \frac{-1}{\left(1 - \frac{\pi^2 v^2}{2}\right)},$$

where $v = s/\mu$.

Appendix B

Letting $\phi(\tau)$ be a unity impulse function at $\tau = a_s$, equation (12) becomes

$$\int_0^\infty e^{-r\tau}(1 + K)\delta(\tau - a_s)\,d\tau = (1 + K)e^{-ra_s}$$

If the density-dependent effect is compensatory, $1 + K$ is negative, and r must be complex. Letting $r = x + iy$ and solving $e^{-ra_s}(1 + K) = 1$ for the value of K which yields a purely imaginary root (K'), we obtain for the real and imaginary parts

$$\cos(a_s y) = \frac{1}{1 + K'} \quad \text{and} \quad \sin(a_s y) = 0,$$

respectively. The latter is solved by $a_s y = n\pi$ $(n = 0, 1, \ldots)$ which implies (for $n = 1$) the period $T = 2\pi/y = 2a_s$. Since $\cos(\pi) = -1$, $K' = 0$. Any value of $K < 0$ leads to unstable oscillations.

If the density-dependent effect is depensatory $1 + K$ is positive and r is real. Its value is

$$r = -\frac{1}{a_s}\left(\ln\left(\frac{1}{1 + K}\right)\right).$$

Thus $r = 0$ for $K = 0$ and decreases monotonically with K.

Predation by Freshwater Seals on the Fish Community of Lower Seal Lake, Quebec

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POWER, G., AND J. GREGOIRE. 1978. Predation by freshwater seals on the fish community of Lower Seal Lake, Quebec. J. Fish. Res. Board Can. 35: 844–850.

The presence of freshwater harbor seals (*Phoca vitulina*) in Lower Seal Lake, Quebec, has drastically modified the lake's fish community. Lake trout (*Salvelinus namaycush*) are the most affected; they are small (rarely exceed 55 cm fork length), their growth rate is faster than in neighboring lakes, their longevity is greatly reduced, the age at sexual maturity has been halved, and individual fecundity per unit weight has increased at the expense of egg diameter. Brook trout (*S. fontinalis*), the dominant fish species in the lake, show evidence of high mortality rates in the lake, but are protected during the vulnerable spawning period because their spawning sites are dispersed in tributary streams. Rough calculation suggests the seal population is small and that it consumes the lake's potential yield of fish annually.

Key words: predation, freshwater seals, *Phoca vitulina*, *Salvelinus namaycush*, *Salvelinus fontinalis*

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La population de phoques (*Phoca vitulina*) qu'on retrouve dans le lac des Loups Marins, Québec, affecte grandement la communauté piscicole du lac. Le touladi (*Salvelinus namaycush*) est l'espèce la plus affectée : peu d'individus atteignent 55 cm de longueur à la fourche; les taux de croissance est supérieur à ceux des lacs voisins et la longévité est grandement diminuée. La maturité sexuelle est atteinte deux fois plus rapidement. Le nombre d'oeufs par unité de poids s'est accru, alors que le diamètre moyen des oeufs a diminué. L'omble de fontaine (*S. fontinalis*), l'espèce dominante du lac, semble subir de forts taux de mortalité, sauf en période de fraye alors que les géniteurs occupent les tributaires. Des calculs approximatifs suggèrent que la population de phoques est faible et que sa consommation annuelle égale la récolte potentielle de poissons du lac.

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Low (1898), Doutt (1942, 1954), and Harper (1961) have recorded the presence of harbor seals (*Phoca vitulina*) in interior lakes in the Ungava peninsula. In the Northwest Territories, Mansfield (1967) and Beck et al. (1970) have reported the same species in lakes discharging along the west coast of Hudson Bay and in southwestern Baffin Island. These seals could be either transient migrants from coastal populations or exclusively freshwater residents. Arrival in freshwater may have been recent or they could be glacial relicts whose origins date back 3000-8000 yr. This latter view has prevailed for the populations in Lower and Upper Seal lakes, which occur at altitudes of 260 and 300 m above sea level. Doutt (1942), on the basis of specimens from Lower Seal Lake, proposed a separate subspecies, *Phoca vitulina mellonae*, and used the degree of speciation as evidence of long isolation of this population. More recent work by Mansfield (1967) has shown the basis for separation to be questionable, so that the time of origin and period of isolation remain in doubt.

There appear to be no comments in the literature on the possible effect of freshwater seal predation on fish stocks, although seals are known to be voracious fish predators. However, Doutt (1942), on the basis of Indian information, mentioned that fishing was known to be poor in the Seal Lakes of Quebec.

The purpose of this paper is to show that changes in the fish community of Lower Seal Lake, compared with neighboring lakes, were caused by predation by seals. Our observations suggest that Lower Seal Lake has been inhabited by seals for a considerable time and that several other lakes, namely Clearwater Lake and Minto Lake, which are listed by Mansfield (1967) as possible seal lakes, do not support seals at the present time.

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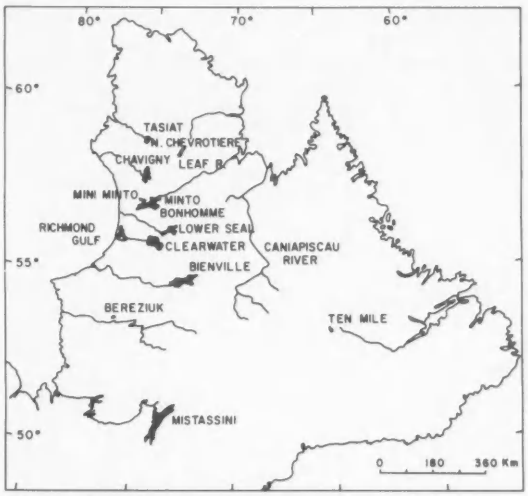

FIG. 1. Locations of 12 lakes in northern Quebec and Labrador where fisheries surveys have been conducted.

Materials and Methods

The data used in this paper were collected during fisheries surveys in northern Quebec and Labrador. Locations are identified in Fig. 1. Included are results obtained in 1973 from Lake Bereziuk by a field party working for the James Bay Energy Corporation. In 1974 Environment Canada personnel investigated Ten Mile Lake, Labrador (Parsons 1975). In 1975 a Hydro Quebec team, under the direction of G. Shooner, worked in Lake Bienville. During the same season, the Centre d'Études Nordiques (CEN), Laval University, surveyed the western portion of Lake Minto and a second group worked in an unnamed lake "Mini Minto" immediately to the north. In 1976 Lake Bonhomme, just south of Lake Minto, was investigated. Six to ten weeks of summer fieldwork was involved in each of the above CEN locations. In 1976 a CEN team spent 8–10 d at Clearwater Lake, Lake Chavigny, Lake Tasiat, North Chevrotière Lake (a small lake north of Lake la Chevrotière), and Lower Seal Lake.

In all the above surveys the purpose was to describe the fish communities. Nylon gill nets of mesh size 38–140 mm (12.5-mm increments), 30–45 m long, 1.8 m deep, were the principal method of fish collection. Nets were set on the bottom, either fished singly from shore or arranged in gangs of several nets tied end to end. Equal effort was not expended with each mesh size, but in every study the nets were deployed in an attempt to collect a representative sample of the kinds and numbers of fish present in each lake. Nets were fished singly from shore in the CEN work, as few or no fish were taken offshore when the nets were fished in gangs. Deep-water sets were also very unproductive.

Routine analysis of the catch in every study involved measurement of fork length (millimetres) and weighing to the precision allowed by field balances, i.e. generally to the nearest 5 g for fish under 500 g and to the nearest 50 g for heavier fish. Scales or otoliths, and occasionally other suitable structures, were collected for age determination. Since aging presents difficulties in northern fish populations, as pointed out by Johnson (1976) and Power (1978), most of the age data used in this paper were obtained from our own interpretation of otoliths. However, some of the comparative data on age structure of brook trout populations came from unpublished manuscripts, the authors of which used scales, otoliths, or both structures for age determination. Fish were sexed by examination of the gonads, and ovaries of ripe or almost ripe fish were preserved in 5–10% formalin for later weighing and measurement of egg diameters and counting. Fecundity was estimated from total counts or weighed samples of ~10% of each ovary.

Results

Observations on Seals

Seals were observed on three occasions. Two sightings were in a small tributary stream connecting Lower Seal Lake with an unnamed lake to the south. One seal descended a shallow rapid into a deeper pool, passing within 2–3 m of an observer, and returned by the same passage. Another seal was seen near the foot of a rapid in a lake-like section of the stream. The third sighting was in the southwestern basin of the main lake. On each occasion little or no noise had been made by the observers. Although many hours were spent on the lake in a powered boat no sightings were made. More recently, Dr R. Bider (personal communication) saw seals on the ice in the spring of 1977 while carrying out aerial surveys of birds. The only other evidence of seals in the lake was indirect. On four occasions nets were stripped of their catch, but as other aquatic mammals could have been responsible, this evidence is not conclusive. Note, however, that on only one other occasion in 1976 was a catch tampered with, and that was by a pair of river otters (*Lutra canadensis*) in Lake Chavigny.

Fish Community

Table 1 shows that of the 10 lakes listed Lower Seal Lake stands out as being different. The dominant fish species is the brook trout (*Salvelinus fontinalis*), which accounts for two thirds of the fish taken in this lake. The lake that is geographically closest, Clearwater Lake, is clearly dominated by lake trout (*S. namaycush*). Both lakes appear similar: conductivity of Clearwater Lake (July 2, 1976) 16 μmhos, Secchi disc 17 m; conductivity of Lower Seal Lake (August 14, 1976) 13 μmhos, Secchi disc 7 m. Both lakes have large areas of shallow water.

In Lower Seal Lake, the lake trout has been most affected by the seals; instead of being the top carnivore it is the seal's prey and the population exhibits all the effects associated with heavy exploitation. Figure 2 shows that except in Lower Seal Lake, the majority of lake trout caught were between 45 and 65 cm fork length. In Lower Seal Lake few trout were taken above 45 cm. The lakes that were fished most intensively, Bonhomme and North Chevrotière, were the two smallest lakes in the study and were the lakes in which the

TABLE 1. Sample size and percentage by number of each fish species captured in surveys of several northern Quebec and Labrador lakes, listed from north to south.

Lake	*Salvelinus namaycush*	*S. fontinalis*	*S. alpinus*	*Coregonus clupeaformis*	*C. artedii*	*Prosopium cylindraceum*	*Lota lota*	*Catostomus catostomus*	*Couesius plumbeus*	*Esox lucius*	*Catostomus commersoni*	Total sample
Tasiat	73.8	2.8	4.6	1.8	11.2	3.7	—	1.8	—	—	—	107
N. Chevrotière	35.6	0.6	0.2	—	5.8	3.0	0.6	54.2	—	—	—	640
Chavigny	76.1	6.2	8.4	—	4.4	0.9	—	4.0	—	—	—	226
Mini Minto	69.3	5.5	14.4	—	—	7.9	1.0	0.5	1.3	—	—	1281
Minto	72.4	5.0	3.7	2.9	3.5	9.1	0.6	2.5	—	—	—	1026
Bonhomme	50.0	24.0	20.5	—	—	4.9	0.3	0.3	—	—	—	708
Lower Seal	18.1	65.4	—	4.0	0.5	6.9	0.2	4.3	—	—	—	344
Clearwater	74.4	9.4	—	8.3	0.5	3.8	2.2	1.1	—	—	—	180
Bienville	8.2	6.0	—	24.0	—	4.9	0.4	47.5	—	1.7	6.9	1043
Ten Mile	20.4	3.9	—	20.9	—	12.3	0.2	—	—	16.9	25.0	679

mean size of trout taken most closely approached that of Lower Seal Lake.

The difference between the lake trout of Lower Seal Lake and those of other lakes is even more marked when age is considered. The mean age of 63 lake trout sampled in Lower Seal Lake was 5.8 yr, range 4–8. Northern lake trout populations usually include many large old individuals. In Clearwater Lake, adjacent to Lower Seal Lake, 133 lake trout had a mean age of 20.6 yr, range 4–51; in Lake Tasiat to the north the values for 79 specimens were 18.0 yr, 4–45. In Lake Mistassini, which is considerably farther south and subject to exploitation by an Indian fishery, the mean age of 496 lake trout examined by Dubois and Lagueux (1968) was 11.7 yr, range 3–24. The absence of old fish in Lower Seal Lake is very marked, this segment of the population having apparently been eliminated by seal predation.

The lake trout in Lower Seal Lake show a number of compensatory responses to seal predation, although not all of these are so clear or dramatic as the effects just described. Growth is more rapid than in the adjacent Clearwater Lake or in Lake Tasiat (Fig. 3). Lake trout aged 5 and 6 yr in Lower Seal Lake are the same size as 9- and 10-yr-old fish from these lakes. Statistical comparisons were difficult because collections from Clearwater Lake and Lake Tasiat were obtained earlier in the summer and contained few young fish. A conservative comparison, which eliminated the problem of sampling time, showed that 5-yr-old lake trout (25) in Lower Seal Lake were significantly larger, 351 mm, than 6-yr-old fish (4), 229 mm, in Clearwater Lake ($t = 7.51$, $P < 0.001$) or 6-yr-old fish, (6) 266 mm in Tasiat Lake ($t = 6.08$, $P < 0.001$). Growth in Lower Seal Lake is similar to that reported by Dubois and Lagueux (1968) for Lake Mistassini, which is considerably farther south.

The most conspicuous adaptation is in the age at sexual maturity (Table 2). In adjacent and more northerly lake trout populations, maturity is attained at age 12 or older. In Lake Mistassini a few fish mature at ages 7–9, while in Lower Seal Lake they mature at ages 5–6. Related to this is the size of mature fish which is significantly less in Lower Seal Lake and affects individual fecundity. The proportions of mature fish at each age can be interpreted to indicate that female fish in Lower Seal Lake generally survive to spawn only once. By contrast, the reproductive pattern is for females to spawn in 2 yr out of 3 in Lake Mistassini, in alternate years in lakes in the region of Lower Seal Lake, and as infrequently as every 3rd yr in lakes farther north. There are also some adjustments in individual fecundity that increase the reproductive potential of the lake trout in Lower Seal Lake. These involve an increase in the number of mature eggs per gram of body weight, brought about by a decrease in egg diameter. The upper panel of Fig. 4 shows the difference in body length and egg production between the Lower Seal Lake mature females and those from other lakes, while the lower panel shows the difference in egg diameter, which must be related to the maturation cycle and the period when the samples were collected for valid comparison.

The lake whitefish (*Coregonus clupeaformis*) was not common in Lower Seal Lake; only 14 specimens were taken, all small. These can be compared with samples from other lakes by arranging in 4-cm-long intervals. For Lower Seal Lake the mode and the number in modal class/sample size were 31 cm and 6/14, respectively. Samples from other lakes gave the following: Lake Minto, 55 cm, 12/30; Clearwater Lake, 55 cm, 8/15;

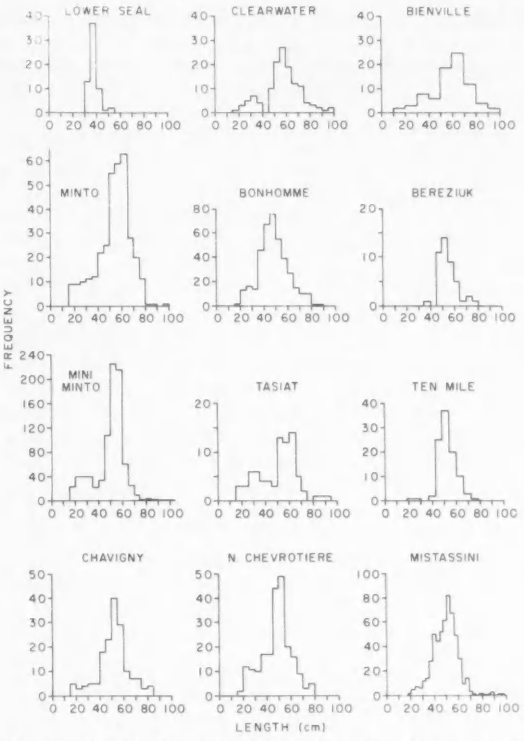

FIG. 2. Length-frequency distributions of lake trout captured during surveys of 12 northern Quebec and Labrador lakes.

TABLE 2. Numbers of immature and mature lake trout observed in samples from northern Quebec. I, immature; M, mature male; F, mature female.

	Age-group								
	0–9			10–19			≥20		
Lake	I	M	F	I	M	F	I	M	F
Tasiat	15	—	—	17	6	3	12	15	11
N. Chevrotière	26	—	—	47	16	5	57	12	8
Chavigny	15	—	—	69	9	7	45	14	11
Lower Seal	20	28	15	—	—	—	—	—	—
Clearwater	14	—	—	27	11	9	23	26	23
Mistassini	101	19	3	78	84	57	8	20	9

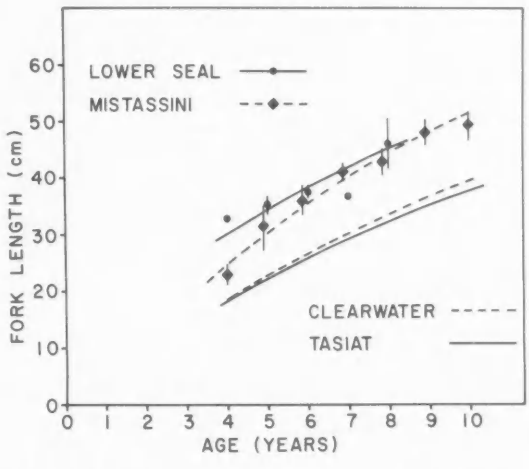

FIG. 3. Growth of lake trout in Lower Seal Lake compared with growth in Lake Mistassini (after Dubois and Lagueux 1968), Lake Tasiat, and Clearwater Lake (after Power 1978). Vertical bars on the upper curves are 95% confidence intervals where sample size allows calculation.

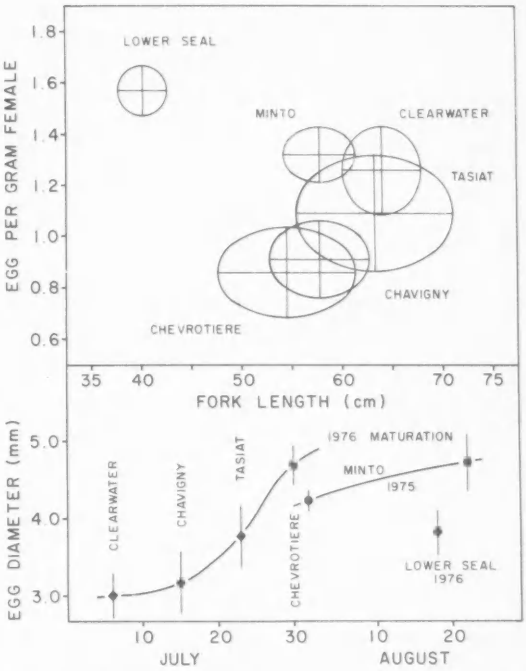

FIG. 4. Differences between the female reproducing segment of the population of lake trout in Lower Seal Lake and those of other Quebec lakes. The upper panel contrasts the length and egg production per gram of body weight; the lower panel shows the seasonal pattern of increase in egg diameters during the maturation cycle. In each panel, horizontal and vertical bars represent the 95% confidence intervals about the means.

and Ten Mile Lake, 47 cm, 30/100. The fish in Lower Seal Lake were all young; the growth was similar to that of lake whitefish in Lake Minto and also probably Clearwater Lake.

The brook trout (*S. fontinalis*) was the dominant fish species in Lower Seal Lake (Table 1). The age-

TABLE 3. Number of fish per unit effort and weight in grams of fish per unit effort from five Quebec lakes surveyed in 1976. The lakes are listed in order of sampling during July and August.

Lakes Fishing effort	Clearwater 37	Chavigny 39	Tasiat 32	Chevrotière 36	Lower Seal 38
Numbers					
Salvelinus namaycush	3.51	4.18	2.44	6.11	1.63
S. fontinalis	0.46	0.36	0.09	0.11	5.26
S. alpinus	—	0.49	0.16	0.03	—
Coregonus clupeaformis	0.41	—	0.06	—	0.37
C. artedii	0.03	0.26	0.38	0.86	0.05
Prosopium cylindraceum	0.19	0.05	0.13	0.53	0.63
Catostomus catostomus	0.03	0.23	0.06	9.58	0.42
Lota lota	0.05	—	—	0.11	0.03
Total no.	4.68	5.57	3.32	17.33	8.39
Weight (g)					
Salvelinus namaycush	8 395	7 128	4 451	9 222	1 043
S. fontinalis	106	43	9	11	1 439
S. alpinus	—	120	238	20	—
Coregonus clupeaformis	1 110	—	243	—	196
C. artedii	2	54	36	128	3
Prosopium cylindraceum	44	14	30	255	89
Catostomus catostomus	9	51	36	8 171	80
Lota lota	9	—	—	64	2
Total wt	9 675	7 410	5 043	17 871	2 852

frequency distribution of the catch (229) was typical of lake-dwelling populations of this species, age-group 3+ being most abundant but including good numbers of fish aged 2+ and 4+. There were few 5+ trout and only one 6+. The fish were in good condition and appeared to be exploiting fully the lake habitat. Growth was rapid but it is difficult to know whether it was exceptional because of the great variability in growth of this species in the northern environment.

Discussion

The results leave little doubt that seal predation has modified the fish community in Lower Seal Lake. The species most obviously affected is the lake trout. In northern lakes without seals, modal sizes in catch samples vary from 50 to 70 cm (Johnson 1976; these results) and populations contain many old fish. Reproduction begins at age 10–14; females do not spawn every year; males tend to spawn more frequently and mature younger than females. Under the influence of seal predation, the lake trout population displays an almost classic response to overexploitation. It is not known whether the population is existing near the limit of its resilience to predation; the low abundance of lake trout suggests it might be. There are probable limits to compensatory responses; for example, reduced egg diameter, allowing increased individual fecundity, is only adaptive providing it is not offset by increased larval mortality. Lake whitefish populations may be similarly affected by seal predation, but the results of this study were insufficient to support a definite conclusion. The brook trout has become the dominant fish species in Lower Seal Lake, occupying the niche left vacant by the reduced biomass of the previous two species. Seal predation has selected against species that are lake spawners and whose reproductive behavior results in aggregations of large mature fish at specific times and places in the lake. These species tend to attain large size and may live to an age in excess of 40 yr in neighboring lakes that lack seals. The brook trout, by contrast, is a stream spawner. Its spawning sites are widely dispersed, and many will be located in small streams inaccessible to seals. The young fish pass their first 2–3 yr in streams, where again they will be relatively immune to seal predation. The age structure of the trout sampled in the lake, and their size, show that they grow rapidly but are subject to heavy mortality. In brook trout populations sampled in the vicinity of Lower Seal Lake, fish older than 6+ yr are normally present and the mortality rate among older fish is usually less (Lee 1969; Coleman 1970; Dutil 1976; Hazel 1976).

Doutt (1942) reported that the Indians considered the fishing poor in Lower Seal Lake. For a native this may simply have meant a lack of large fish, a situation confirmed by our own observations. It could equally have implied a poor catch per unit effort. In 1976 five lakes were surveyed starting with Clearwater Lake at the beginning of July and finishing with Lower Seal Lake in late August. While dates differ, the same gear and approximately the same effort was expended in each lake. The catch per unit effort (one 30-m net/d), expressed as number and weight of fish (Table 3), shows considerable differences between lakes. The small shallow

tundra lake, North Chevrotière, had by far the highest catches, while Lower Seal Lake was second highest in numbers per unit effort but least productive in weight per unit effort owing to the presence of many small fish. Since weight is important when fish are being caught to eat, this evidence supports Indian opinion that the Seal Lakes have a low fishery potential.

The origin of seals in Lower Seal Lake has been discussed by Doutt (1942) and Mansfield (1967) but has not really been settled, although Mansfield's interpretation of the evidence is perhaps the most conservative; i.e. that before the advent of the rifle, coastal populations of the harbor seal made frequent summer migrations into freshwater rivers and lakes. Passage up some rivers, e.g. the Leaf and the Larch, presented no serious obstacle to seals, allowing small populations to become established entirely in freshwater. With the advent of the rifle some of these coastal populations were subsequently eliminated leaving a few isolated populations in the lakes. In support of this hypothesis Mansfield presents morphological data that show that Doutt's material from Lower Seal Lake falls within the normal range of variation of coastal populations of *P. vitulina*. More recently Beck et al. (1970) described a seal from Edehon Lake in the Thlewiaza River, N.W.T. Although it did not differ from other specimens of the harbor seal taken in the arctic, the coronoid process of its lower jaw was long, and this was the characteristic used by Doutt (1942) to establish the subspecific distinction of the Lower Seal Lake specimens *P. v. mellonae*.

Evidence derived from our observations on the fish in Lower Seal Lake is difficult to interpret in terms of a time scale. Selection against large size and late sexual maturity has gone on long enough to alter very significantly the lake trout population. If this can occur in several generations, the seals may only have occupied the lake for 100s of years rather than 1000s as suggested by the proponents of the glacial relict hypothesis. If as Mansfield (1967) believes, seals have been eliminated from Lake Minto (and perhaps Clearwater Lake) since the advent of the rifle, then reversion of the lake trout to the role of dominant predator can occur quickly. There is no evidence of seal predation on the fish of either of these lakes today. If traces of past seal activity in Lake Minto were sought, one might use as evidence two female lake trout, both under 55 cm fork length with exceptionally high egg production and one mature at 39 cm fork length, taken in the present study; at the best such evidence is extremely tenuous.

In discussing seal predation in inland lakes it is reasonable to demand what kind of impact might be anticipated from a small herd of animals in a large lake. The size of the Lower Seal Lake seal population is unknown, but Low (1898) reported Indian kills of the order of 30/yr. To sustain such a kill a population of several hundred would be needed. Boulva (1973) estimated the annual sustainable yield of the postwhelping populations of harbor seal in eastern Canada was about 5%, which gives a minimum estimate of 600 seals in Lower Seal Lake. Another way to estimate the seal population is to assume that it has stabilized at the carrying capacity of the environment; the seals' impact on the fish stocks supports this contention. Boulva (1973) provided an energy budget for maritime populations that gives an estimated fish consumption of 583.45 kg/seal per yr. The potential fish yield for lakes in the vicinity of Lower Seal Lake is about 200 kg (km^2/yr) (Power and LeJeune 1976). The area of Lower Seal Lake is 500 km^2, providing a total yield of 10^4 kg/yr. This could sustain a seal population of perhaps 200 if some of the fish consumed originated in tributaries to the lake. If this is accepted, Low's (1898) estimate of the kill appears too high. These figures clearly demonstrate that only large lakes can sustain populations of freshwater seals and that even then, seal populations must remain small. In terms of preference for food, lake trout (5) and lake whitefish (1) were reported in the stomach of the freshwater seal examined by Beck et al. (1970). In Lower Seal Lake, as a result of modification of the fish community, brook trout are also taken. One of the seals observed in 1976 was clearly hunting brook trout congregated below the rapids of a small stream.

The fish community of Lower Seal Lake might provide a forecast of the effects of a sustained commercial fishery in a northern lake. Such fisheries preferentially select large lake trout and lake whitefish. The long-term effects are likely to be similar to those of seal predation: reduction in average size and age at maturity of the target species and an increase in smaller species able to exploit the habitat no longer fully occupied by these species.

In summary, the seals of Lower Seal Lake, Que., have created a unique situation. The question of their origin in time remains unanswered, but their predation has drastically modified the fish community and perhaps had other repercussions on the aquatic community. The Seal Lakes warrant further study, but the seals should be carefully protected from undue and unnecessary attention. Consideration of the potential fishery yield indicates the seal population must be small.

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Population Estimates of Sockeye Salmon (*Oncorhynchus nerka*) in a Fertilized Oligotrophic Lake

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ROBINSON, D. G., AND W. E. BARRACLOUGH. 1978. Population estimates of sockeye salmon (*Oncorhynchus nerka*) in a fertilized oligotrophic lake. J. Fish. Res. Board Can. 35: 851–860.

Pelagic juvenile sockeye salmon (*Oncorhynchus nerka*) populations were studied in Great Central Lake, British Columbia, during 1969–76 to determine the effect of nutrient enrichment upon their growth and survival. Data for population estimates were collected concurrently by a high-frequency echosounder, and a midwater trawl whose efficiency was inversely related to ambient light above about 1.9×10^{-5} lx. Echogram counts supplemented by trawl catches yielded estimates with low variance, good resolution between age-groups, and indicated close correlation between numbers of spawners and resultant progeny within respective treatments. Survival to the fall for the treated 1969–72 brood years averaged 11.65% (range 11.11–12.81%) of potential egg deposition compared to 3.5% for the pretreatment 1968 brood year fish; 2.73 and 6.29% for the posttreatment 1974 and 1975 brood year fish. A carry-over of fertilization effects on the immediate posttreatment 1973 brood year may have induced a cyclic pattern on the survival of the two succeeding year-classes. The relatively consistent annual production of age 0+ sockeye may be due to the inherent stability of inlake spawning and incubation coupled with the low predation rates. The conservative estimate of a 2.5 increase in survival relative to the natural level indicates a positive response to enhanced feeding conditions caused by the fertilization of this oligotrophic lake.

Key words: sockeye, survival, Great Central Lake, fertilization, enhancement, acoustic estimates, townet efficiency

ROBINSON, D. G., AND W. E. BARRACLOUGH. 1978. Population estimates of sockeye salmon (*Oncorhynchus nerka*) in a fertilized oligotrophic lake. J. Fish. Res. Board Can. 35: 851–860.

Nous avons étudié, au cours de 1969–76, les populations de jeunes saumons nerka (*Oncorhynchus nerka*) prélagiques dans le Grand lac Central, Colombie-Britannique, afin de déterminer l'effet d'un enrichissement de substances nutritives sur leur croissance et leur survie. Les données qui ont servi aux estimations de population ont été cueillies simultanément par un sondeur à écho à haute fréquence et un chalut pélagique dont l'efficacité était en relation inverse de la lumière ambiante au-dessus d'environ 1.9×10^{-5} lx. Les dénombrements sur les échogrammes aidés des captures par le chalut donnent des estimations à faible variance, une bonne séparation entre les groupes d'âge et une étroite corrélation entre le nombre de reproducteurs et leur progéniture à l'intérieur de leur traitement respectif. La survie jusqu'en automne des poissons des pontes de 1969 à 1972 où le traitement a été appliqué a été en moyenne de 11.65% (extrêmes de 11.11 à 12.81%) du nombre possible d'oeufs déposés. Ceci peut se comparer à 3.5% constatés chez les poissons de la ponte de 1968 avant traitement, à 2.73 et 6.29% pour les poissons de la ponte de posttraitement de 1974 et 1975. Les effets de la fertilisation continuèrent de se faire sentir sur la ponte de 1973 qui suivit immédiatement le traitement et que ceci déclencha un cycle dans la survie des deux classes d'âge suivantes. On est d'avis que la production annuelle relativement uniforme de saumons nerka d'âge 0+ peut être due à la stabilité inhérente de la ponte et de l'incubation dans le lac, couplée à de faibles taux de prédation. L'estimation conservatrice d'une augmentation de survie de 2.5 par rapport au niveau naturel indique une réponse positive à une amélioration des conditions alimentaires produite par la fertilisation de ce lac oligotrophe.

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THE fertilization of Great Central Lake, Vancouver Island, British Columbia, was undertaken to test the hypothesis that the addition of inorganic nutrients to an oligotrophic lake would increase primary productivity and, ultimately, enhance the production of the juvenile sockeye salmon (*Oncorhynchus nerka*) which utilize the pelagic waters of the lake as a nursery area. To this end, 100 tons of fertilizer were added each year from 1970 to 1973 in lots of 5 tons/wk starting at the onset of thermal stratification.

Fertilization significantly increased primary production (Parsons et al. 1972) and zooplankton standing stock (LeBrasseur and Kennedy 1972). Growth rates of young sockeye in the lake increased such that the average weight of the fish at the onset of winter was 30–92% greater than years when the lake was unfertilized (Barraclough and Robinson 1972; Robinson and Barraclough 1972, 1973, 1975a, b).

To assess the overall effect of fertilization on sockeye salmon production, it was necessary to estimate the absolute number of young sockeye of each year-class inhabiting the lake and hence the relative survival rates. This paper reports the method developed toward this end and the observed results.

While it appeared that enhanced feeding with subsequent growth was the mechanism whereby survivorship was increased, feeding and growth were complicated by abiotic and biotic factors that limited the benefits realized by individual fry. The net effect on the population was that production was enhanced more by the increased numbers of fish surviving to migrate seaward than it was by the increase in average weight per migrant. Detailed analysis of these factors are the subject for a later paper.

The earliest in-lake estimates of juvenile sockeye numbers were made by Johnson (1956, 1958), using townet techniques in Babine Lake; catches were weighted by a constant of proportionality based on catch-per-unit effort of a population of known size as established in earlier work on Lakelse Lake. Population estimates based solely on townet data have a large inherent variance (Pella 1964; Mathisen et al. 1973) which appears to be largely the result of assuming constant availability of fish to the net. Echosounders, used in conjunction with townetting, overcame this deficiency to some degree (Gregory and Mathisen 1963; Rogers 1967), but there were significant differences between the apparent availability and the catch of fish which may be the result of the effects of wind and light on the distribution of the fish. Data in this paper indicate this to be an avoidance reaction controlled by light intensity.

Materials and Methods

In Great Central Lake, data were collected concurrently at night using an echosounder and a townet. The effective insonified volume of the acoustic cone was estimated. Echogram counts were used in conjunction with townet catches obtained under a variety of light levels and depth ranges to establish the efficiency of the net. Population estimates were then made on the basis of the acoustic data supplemented by townet data. The method is basically a digital counting system (Dowd 1969) with increased depth partitioning but without the automated signal processing.

Townet samples were used to provide additional information on growth, feeding, and age structure of the populations under study, and they permitted resolution of age-groups when sizes and depths of fish overlapped and were acoustically irresolvable, a feature common in Great Central Lake from about midsummer to smolt emigration. A calibrated townet also allowed the range of population estimates to be extended into areas of high density or pelagic surface waters. The efficiency of the net appeared to be constant over all natural densities of fish, whereas the acoustic system eventually encountered densities above which coincidental counts led to an underestimate of the numbers present, an error that increased in magnitude with density above some initial value.

The concurrent use of both echosounder and townet permitted the most useful features of each method to be exploited and provided checks against the internal variation in efficiency of one system relative to the other.

The sounder used from early 1970 onwards was a Furuno FNV-3000 capable of operation at 28 or 200 kHz. The transducers were mounted in the hull of the 11-m, diesel-powered *Decibar*. Incoming target information was recorded on moist paper to produce an echogram and could be simultaneously flashed on an integrated cathode ray tube. All data were collected at 200 kHz using a circular Barium titanate transducer. Peak output power was 1.6 kW; recorder gain was standardized at 4.7 on a scale of 1–6. An integrated voltmeter facilitated periodic checks on the output of five internal circuits. Pulse width was usually set at 3 ms. Greater resolution was achieved during times of high target density by selecting a shorter pulse width of 1 ms. A third alternative, 0.5 ms, was not used as it was found to produce confusion in differentiating between bona fide targets and "noise" spikes.

The sockeye were caught with a midwater trawl having a mouth opening 3.0 m wide by 6.1 m deep (Barraclough and Robinson 1972). Modifications to the towing bridles enabled this net to be operated at all depths at which targets were recorded on the sounder. Towing speed was set between 0.66 m/s and 1.10 m/s, with the majority of tows at the latter speed. Variation of towing speed within this range did not produce significant differences in the efficiency of the net. Sockeye caught were immediately preserved in 10% formalin. Numbers captured, age, and size were determined later in the laboratory.

Light was measured with an IL 600/660 low level photometer. The Photomultiplier was filtered to have a peak response at a frequency of 560 nm and was mounted in a submersible unit connected to the photometer via an 80-m cable. During operations this unit was suspended 3 m out from the hull of the vessel.

Determination of Effective Insonified Volume

The first step in deriving an absolute population estimate was to calibrate the effective diameter of the acoustic cone at those depths at which sockeye occurred. This was done empirically as described by Nunnallee (1973), a brief résumé of which is given below:

If the fish targets are assumed to be uniformly distributed within a depth stratum and to have small, random movements with respect to the acoustic cone, then counting the

TABLE 1. Cone diameter and beam angle calculated from average number of isonifications per target ($\bar{c}$) for five depths. Number of replications at each depth is in parentheses.

Depth (m)	$\bar{c}$	Cone diam (m)	Beam angle
10	1.65 (4)	1.57	8.94°
20	3.25 (5)	3.10	8.80°
30	5.17 (3)	4.94	9.32°
40	7.10 (2)	6.76	9.60°
50	7.92 (2)	7.54	8.58°

number of insonifications per target moving through the cone at a given depth yields an estimate of the expected chord length, $E(c)$, of the cone at that depth by the equation

$$E(c) = \frac{v \cdot \bar{c}}{R} \tag{1}$$

where v is the boat velocity in metres per second (1.10 m/s), $\bar{c}$ is the calculated average number of insonifications per target, and R is the repetition rate of the sounder in pulses per second (1.47 p/s). Also, since

$$\text{cone diameter at a depth } d = \frac{4}{\pi} \cdot E(c)_d \simeq d \tan \phi, \tag{2}$$

the effective cone diameter and the associated beam angle ϕ at a depth d may then be calculated.

In November of 1974, 1975, and 1976 counts were made of the number of insonifications per target moving through the acoustic cone at several depths ±2 m (Table 1). Each sample was composed of the counts from 100 targets as displayed on the integrated cathode ray tube, the amplitude level of which was set so that the limit of target detection coincided with that of the echogram. November was chosen to remove the chance of adult sockeye contributing artificially high counts; the adults by that time were inshore on the spawning beaches. Coincidence within the counts was avoided by choosing areas within the lake having low enough target densities at the calibration depth. The data for the 3 yr were not significantly different and were therefore combined.

Estimation of Townet Efficiency

Townet efficiency was estimated by calibrating fish catch against echogram estimates of the population available to the net. Echosounding and townetting were done concurrently, the net being fished at a series of depths. Included in the analyses were the results of station tows made for population estimates and replicate tows made to investigate sampling variance.

Light readings were taken each night at the beginning and end of sampling when constant light conditions prevailed, more frequently if light conditions varied during the sampling. Whenever possible, nights were chosen in which light conditions would tend to be uniform throughout the sampling period. Tows at various depths were replicated for light conditions ranging from full moon and clear sky (light level 8.6×10^{-2} lx or 8×10^{-3} foot candles) to dark of the moon with heavy overcast ($<1.1 \times 10^{-4}$ lx or 1×10^{-5} foot candles, the lower limit of detection for the photometer).

To estimate the population of fish available to the net, the echogram from a particular tow was partitioned into a 6-m depth stratum; that is, 3 m above and below the calibrated center of the net. Twice replicated counts were made of all bona fide marks within this stratum, the average of which was taken to be the "count of marks" for the tow. Only marks that had their origins within the stratum were taken to represent available fish. When the count of marks was completed, the townet catch was counted, sorted by age-groups, and the size of the fish measured. This order of data analysis was selected to avoid decisions regarding the validity of marks being influenced by prior knowledge of the actual number of fish caught.

Catches were composed primarily of age 0+ (underyearling) sockeye with the balance normally composed of age 1+ (yearlings). Other fish which were occasionally taken in small numbers were older sockeye, immature residuals and prespawning adults, threespine stickleback (*Gasterosteus aculeatus*), and river lamprey (*Lampetra ayresi*). These occasional fish were usually taken at depths outside the main concentrations of juvenile sockeye. For calculation of townet efficiency, all fish were included in "total catch."

The expected ratio of townet catch to count of marks was calculated, using the net width of 3.0 m and a cone diameter for each depth as estimated using equation 2, with angle ϕ taken to be equal to 8.9°. The observed ratio between "total catch" and "count of marks" was calculated. Townet efficiency was then

$$\text{efficiency} = \frac{\text{observed ratio}}{\text{expected ratio}} \times 100. \tag{3}$$

The amount of light in situ was converted from light in air using extinction curves established for the lake under a wide range of light levels and over all seasons. The curves were adequately described by two straight lines, with an inflection point at about 11 m, at which point light had decreased to one tenth of surface levels. It was also found that light just under the surface was on the average 85% of light in air just above the surface. For depths to 11 m, then

$$L_d = 0.85\, L_a e^{-kd} \tag{4}$$

where L_d is illuminance in lux at depth d in metres, L_a is illuminance in air as measured with the photometer, and the extinction coefficient k equal to 0.2093. For depths >11 m, light decreased by an order of magnitude every 15 m, and

$$L_d = 0.085\, L_a e^{-k'(d-11)} \tag{5}$$

with k' equal to 0.1535.

Population Estimates During 1974, 1975, and 1976

To produce a population estimate, townetting and echosounding were done at six standard fishing stations within the lake. If supplemental townet data were needed, as in 1974, the net was set to coincide with the depth of maximum concentration of fish targets. In addition, depth series were done to establish the ratio of underyearlings to yearlings over the main depth range of the fish. If supplemental townet data were not needed, as in 1975 and 1976, towing depths were set to maximize depth distribution information.

The echogram for each station was partitioned into 6-m depth strata centered around the townet depth as described above, and the number of targets within each stratum counted. If coincidental counts for a stratum were obtained

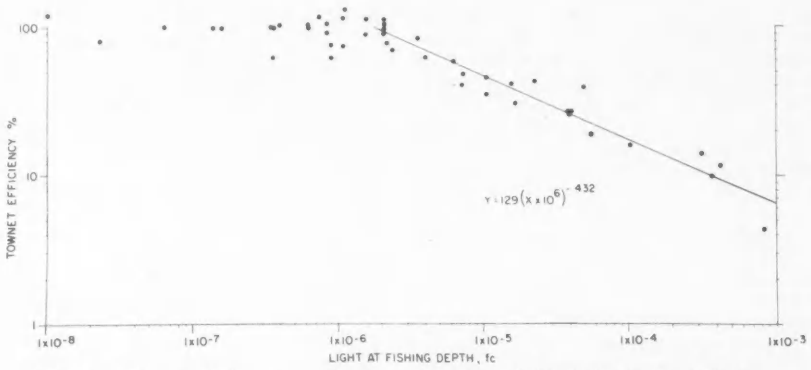

FIG. 1. Townet efficiency as a function of ambient light at the depth of fishing. Regression is for points greater than the approximate response threshold of 1.9×10^{-5} lx (1.8×10^{-6} foot candles) intensity.

due to high density, then the number of fish caught at that depth, corrected for townet efficiency, was substituted. On only one occasion, in 1974, was high density so distributed at a station that coincidental counts occurred in more than one stratum. The count of marks for each stratum was adjusted to correct for cone expansion with depth. This adjusted count was partitioned within each stratum into the proportion of the different age-groups present, based on the results of the depth series of tows, and the results summed to yield a "tow estimate" for each age-group that are present under a 3-m wide column of given length at that station. A "station estimate" was calculated using the ratio between the lake surface area represented by a station and the surface area represented by a sampling run of given duration and speed. The sum of all station estimates yielded a population estimate for the lake.

POPULATION ESTIMATES FOR 1969–73

The above method was applied to echograms collected prior to 1974 to estimate the numbers of sockeye within the lake during the earlier years of the program. The townet and the echosounder were always operated in a standard manner. An empirical examination of the assumption that system output was constant under various partitions was carried out by regressing catch of fish on count of marks. This was, in effect, a test of sounder output since it is unlikely that townet efficiency would have varied under a given set of conditions. After light had been identified as the major component affecting variability in townet catches, the variances within these data were also of value in considering the accuracy to which available light must be measured to estimate townet efficiency within acceptable confidence limits.

Data from which population estimates could be made were limited to those collected from midsummer to late fall, because of seasonal changes in the behavior of the fish, and the winter ice cover. In the spring and early summer, many of the young sockeye remain in the upper few metres of the lake throughout the hours of darkness and thus were not recorded on the echogram. In the absence of quantitative townet data from the surface waters, estimates of abundance made from echograms collected during this period were consistently about one third those produced later in the summer when the fish occupy a narrow band within the thermocline at 10–15 m depth throughout the hours of darkness.

A further restriction was that population estimates could be made within the above period when either densities were low enough to yield accurate counts, or townet data could be used to supplement the echogram data if densities were high. Samples were rejected if a high density of fish was coupled with a logbook entry reporting variable light conditions. These were usually statements referring either to variable cloud cover or to moonlight which was affected by clouds or by periods "in shadow" behind mountains.

As a different sounder was used in the fall of 1969, estimates for that year were derived from townet data weighted with the average depth factor for the appropriate dates from other years. The depth factor, which is quite consistent between years for a given seasonal distribution, is the ratio between the adjusted count of fish at a station and the adjusted count at the towing depth only. This was 2.9 for November and 5.7 for December, and was in good agreement with the factors as calculated from the 1969 echograms (approximately 3 and 6, respectively) collected with an uncalibrated sounder.

The catches of age 1+ sockeye were small and intermittent in 1969 and 1976, suggesting that very low numbers were present. It was felt that a better estimate would be achieved by grouping the results of all tows and taking this ratio to represent the proportion of 1+ fish within the lake. In 1969, 15 of the total 1266 juvenile sockeye caught were age 1+; while in 1976, only 17 out of 3204 were of the older age-group. The numbers of 1+ fish were therefore taken to be 1.20 and 0.53%, respectively, of each total population estimate.

Results and Discussion

EFFECT OF LIGHT ON TOWNET EFFICIENCY

For our sampling system, there is an apparent response threshold at about 1.9×10^{-5} lx (1.8×10^{-6} foot candles) in situ, below which efficiency did not differ significantly from 100% ($Y = 96.6 \pm 8.10$ at 95% confidence level for $N = 21$) (Fig. 1). For light levels greater than the threshold value, the logarithm

TABLE 2. Significant results of regression of catch of fish on count of marks for data prior to 1974. Light categories are 1 — overcast, no moon; 2 — no moon; 3 — some moonlight; 4 — clear, full moon.

Depth range (m)	Weighted mean depth (m)	Light category	a	b	df	F	SE of slope	95% C.I.
9–14	11	1	−43.4	1.71	1,30	102	.169	±.345
9–14	11	2, 3	−6.8	0.461	1,110	146	.037	±.073
9–14	11	4	−1.0	0.123	1,8	23.2	.024	±.055
17–25	20	all	−14.9	0.762	1,29	67.9	.092	±.19
30–50	40	all	−15.0	0.452	1,28	58.9	.058	±.12

of efficiency was inversely proportional to the logarithm of intensity; that is, it obeyed the Weber-Fechner Law. The power curve was chosen to express the highly significant relationship ($F = 355$; $P < 0.001$) in which

$$\hat{Y} = 129\,(X \times 10^6)^{-0.432}, \quad \text{SE}_b = 0.0229. \tag{6}$$

Practical examples of nighttime efficiency at 10 m depth were 100% for overcast sky and dark of moon, 47% for clear sky and dark of moon, and 6.4% for clear sky with full moon.

This exercise was repeated in 1975, with similar results, except that greater variance in the size distribution of the fish led to increased variance about the mean efficiency at a given light level. This does not affect the total estimate, but does have some effect on the partitioning into age-groups (Robinson and Barraclough unpublished data).

While some errors are inherent in the assumptions regarding cone calibrations and relative sampling volumes of the acoustic vs. the townet systems, these errors produced small changes in the absolute estimates (Nunnallee 1973) and had no effect on the analysis of the relative survival rates.

We tested the assumption that results from previous years agreed with those obtained from 1974 to 1976 (Table 2). Regressions of catch of fish on count of marks were made with the data partitioned by light levels, depth of tow, speed during tow, and years. Only the former two were significant, and data were therefore pooled into light and depth categories.

In the 11-m depth range, the observed slopes for light categories 1 (overcast, no moon) and 4 (clear, full moon) are in close agreement with the expected slopes from equation 6; 1.71 to 1.74 and 0.123 to 0.122, respectively. There is also close agreement in the 40-m depth range, 0.45 to 0.48. No significant difference was found between the observed slopes under light category 2 (no moon) and 3 (some moonlight). This might be expected from the wide and variable range of light conditions covered by these two categories caused by such as broken cloud cover. The combined slope of 0.461 is intermediate between the expected slopes of 0.891 and 0.329 (with category 3 taken to be quarter moon, or $L_a = 1.1 \times 10^{-2}$ lx or 1×10^{-3} foot candles.

The tendency for this combined slope to be low as well as variable is probably a reflection of the sampling strategy of earlier years, which sought to maximize the information from stomach samples. Tows were thus made as soon after the dusk feeding period as possible, often before the onset of full darkness, and sampling of the six stations was done over two or three evenings. That the lowest townet efficiency observed on a given night was usually from the first tow, coupled with the dispersed nature of the targets on the echogram, lends support to the conclusion that many stations were sampled under considerably brighter light levels than as categorized.

In a similar fashion, in the 20-m depth range the observed slope was 0.76 to 0.96 expected at 100% townet efficiency. The difference, which is only just significant, is probably attributable to the effect of light in some of these tows. The data were pooled as those for light categories >1 were too few to show significant differences. Tows in the 40-m depth range were usually done during the winter when overcast conditions prevailed. There is therefore very little likelihood of any light effect, as is supported by the data.

The 95% confidence intervals for the slopes for those depths and light categories used in population estimates (Table 2) range from ±16 to 25%. These may be compared to the limits calculated for the data in Fig. 1; ±8.4% for points $<1.9 \times 10^{-5}$ lx (1.8×10^{-6} foot candles) and ±11% for points $>1.9 \times 10^{-5}$ lx. The increased confidence of these latter is probably due to the greater resolution of the light available in situ.

It was concluded from the above that the sampling efficiencies of the sounder and the townet were in agreement with the calibrations as done from 1974 to 1976, and that estimates of abundance for the earlier years of the program could be made using the same weighting factors and cone calibrations.

JUVENILE SOCKEYE SALMON POPULATION ESTIMATES

The 0+ and 1+ age-classes make up virtually the whole of the pelagic fish population in all years except 1972, when "residual" sockeye were about 0.6% of the total (Table 3).

The main treatment effect which it was necessary to test was that of fertilization on the survival of young sockeye in the lake. The effects of varying spawner

TABLE 3. Population estimates for Great Central Lake for 1969–76. Each estimate is partitioned into age 0+ and age 1+ components on the basis of townet catches. Means ± 2 SE are given for each year excluding November data from fertilized years 1970–73.

Year in lake	Date	Population estimates		
		Total $\times 10^6$	Age 0+ $\times 10^6$	Age 1+ $\times 10^6$
1969	Nov. 18	3.34	3.3	.038
	Dec. 16	4.05	4.0	.046
	Mean	3.7 ± .71	3.7 ± .70	.042 ± .008
1970	July 21	12.0	11.8	.277
	Aug. 11	11.4	11.3	.070
	Sept. 23	12.7	12.6	.116
	Nov. 17	8.83	8.77	.061
	Mean	12.0 ± .751	11.9 ± .757	.154 ± .126
1971	Sept. 14	3.83	2.70	1.13
	Oct. 19	4.24	3.43	.805
	Nov. 16	2.09	1.75	.345
	Dec. 14	2.94	2.41	.534
	Mean	3.67 ± .767	2.85 ± .607	.823 ± .345
1972	July 12	7.20	6.94	.257
	July 26	6.72	6.43	.276
	Aug. 9	8.34	7.95	.334
	Aug. 12	6.34	6.04	.270
	Nov. 22	4.03	3.94	.056
	Dec. 13	6.43	6.30	.130
	Mean	7.01 ± .731	6.73 ± .676	.253 ± .067
1973	Sept. 25	17.5	17.2	.271
	Oct. 23	19.3	19.3	.091
	Nov. 19	11.1	10.9	.222
	Mean	18.4 ± 1.80	18.2 ± 2.10	.181 ± .180
1974	Sept. 17	23.0	20.2	2.85
	Oct. 23	20.7	18.9	1.82
	Nov. 13	24.5	23.1	1.47
	Mean	22.7 ± 2.21	20.7 ± 2.48	2.05 ± .828
1975	Sept. 9	4.59	2.42	2.17
	Sept. 29	5.31	2.71	2.60
	Oct. 6	6.17	3.38	2.79
	Nov. 3	4.78	2.98	1.80
	Nov. 24	4.57	2.80	1.78
	Dec. 2	4.90	2.91	1.99
	Mean	5.05 ± .499	2.87 ± .260	2.19 ± .344
1976	Nov. 2	14.1	14.0	.074
	Nov. 9	13.3	13.2	.070
	Nov. 17	13.0	12.9	.069
	Mean	13.5 ± 0.66	13.4 ± 0.66	.071 ± .003

population sizes and age 1+ carry-overs on the population estimates were removed by calculating mean annual age 0+ survival in percent to the fall of the year from potential egg deposition (Table 4). Potential egg deposition was itself estimated from the number of sockeye in a spawning escapement, adjusted for percentage of females, age distribution, and average fecundity of a given run (Manzer 1972, and personal communication). A single classification Model I analysis of variance (Sokal and Rohlf 1969) on the survival rates gave the following results:

TABLE 4. Mean yearly inlake survival from potential egg deposition (P.E.D.) of age 0+ sockeye, with treatment means.

Unfertilized			Fertilized		
Year	P.E.D. $\times 10^6$	Survival %	Year	P.E.D. $\times 10^6$	Survival %
1969	105	3.5	1970	108.	11.11
1974	338	6.13	1971	25.5	11.16
1975	105	2.73	1972	58.5	11.51
1976	213	6.29	1973	143.	12.81
Treatment means		4.66			11.65

Source of variation	df	Mean square
Between treatments	1	69.3***
Within treatments (error)	6	1.58

Survival during years of lake fertilization was significantly greater ($F = 41.3$: $F.001\ [1,6] = 35.5$) than during nonfertilization years.

To consider the degree to which survival was enhanced, the data in Table 3 must be subjected to a critical analysis of the effect on the estimates of juvenile sockeye population dynamics within and between years, and of the sampling methodology.

The 6-times replicated estimate for 1975 gives a good measure of the variance associated with the acoustic counting method itself, including all spatiotemporal variations over a 3-mo period, in that no supplementary townet data was required to calculate the total fish estimate. Students' t-test indicates 12.6% confidence limits about the mean of 5.05×10^6 fish.

It is pertinent to compare the above results with some collected through the use of an echo-integrating system (Nunnallee and Mathisen 1972; Mathisen et al. 1973). It was concluded that drift within this system contributed to a large extent to the observed variability over a 4-times replicated study (on four consecutive nights) and may have caused the significant differences in the estimated mean density of fish. Either sampling method will record the presence of a fish if the returning signal strength exceeds some minimum detection level. The principal difference between the two methods lies in the subsequent treatment of this signal. The counter merely records the presence of a target whereas the integrator-derived estimate is a function of the amount by which the minimum detection level is exceeded. Echo counting estimates are thus less subject to signal strength variation with a consequent improvement in confidence limits.

High densities of fish necessitated supplemental townet data for one depth stratum in 32 of the 174 station estimates made from 1970 to 1976. Only in 1971, 1975, and 1976 were nighttime densities always

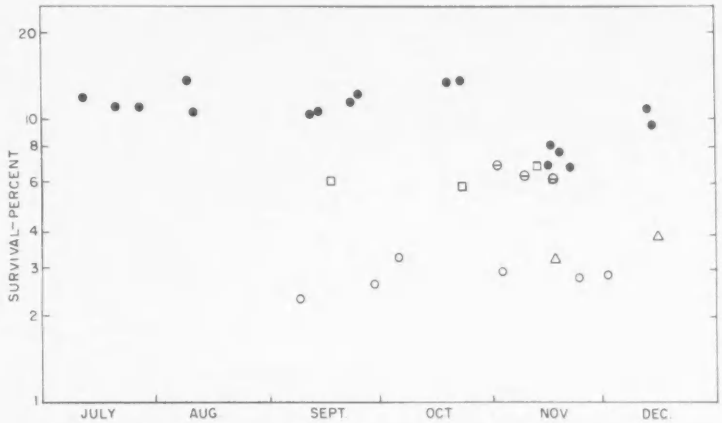

FIG. 2. Percentage survival of age 0+ sockeye in Great Central Lake. Closed circles, fertilized years, 1970–73. Open figures, unfertilized years; △ 1969; □ 1974; ○ 1975; ⊖ 1976.

low enough during the sampling period to permit acoustic enumeration at all depths. For other years, the need for supplemental townet data ranged from 14% of stations in 1972 to 67% in 1974; the need was greatest in summer and decreased through the fall as the fish dispersed in depth.

Where it was required, these supplemental data add another variance component in years of high density; the magnitude of this may be estimated by the data presented in Fig. 1. The variance of the regression equation may be taken to be a fair estimate of the associated variance between catch and count. The proportion of the estimate based on the high density depth may then be considered as a new experiment, and the standard error of the predicted sample mean calculated. Assuming such need for one depth at each of six stations, the 95% prediction limits are ±10% for light category 1, ±16% for light category 2, and ±46% for light category 3. No estimates were made under conditions represented by light category 4. The maximum observed effect of this additional variance may be appreciated by considering the estimate of September 17, 1974, when 63% of the population fitted the above assumption under light category 2, an additional variance component of ±16%.

The use of mean survival of the age 0+ sockeye as a measure of the treatment effect assumes constant availability of the population to the sampling gear, under all conditions during the sampling period; it assumes there is no measurable mortality; and it assumes that survival rates are homogenous within treatments.

With respect to the assumption of constant availability, Fig. 2 shows that the four lowest estimates during fertilized years are clustered together in November, while no such trend is apparent in years of nonfertilization. Further, these estimates were obtained one in each of the four treatment years. Multiple range testing for unequal numbers of replications (Kramer 1956) indicates that as a group these November estimates are significantly less than other months ($4.56 > 3.10$; $P < 0.001$). These observations should be viewed in relation to the sequence of events occurring at this time of year and their probable effect upon the dynamics of the sockeye populations.

Primary production at this time was rapidly declining with a consequent reduction in food intake by the sockeye. Temperatures were dropping as the lake approached isothermy, allowing sockeye to enter surface waters to feed on what food was available. Echo sounder and townet records for November usually indicated some fish in the upper few metres of the pelagial zone at night, which tended to be the smaller of the population. Samples taken from inshore with seines and trapnets tended to be larger than the main pelagic population (Manzer 1976). This is the only time of year juvenile sockeye other than migrating smolts have been taken in the inshore waters of Great Central Lake. They resembled smolts in size and age distribution: the proportion of yearling fish was greater then in the pelagic population, and the 55-mm minimum length of the underyearlings was the same as that of smolts (Barraclough and Robinson 1972). Inshore movement was apparently very limited in unfertilized years despite vigorous sampling (Robinson and Barraclough unpublished data).

These larger fish probably adopted a mode of behavior resembling a smolt in an attempt to maximize food intake. During fertilized years the response was great enough to produce a significant reduction in the population estimate for November. As a consequence, the assumption of constant availability of the population to the pelagial sampling gear is invalid and these data should be rejected from consideration of the degree to which fertilization enhanced sockeye survival.

TABLE 5. Depth distribution of age 0+ and age 1+ sockeye in Great Central Lake, September 18, 1974. All tows were 15 min duration at 1.1 m/s.

Center of depth range (m)	0+ age-group			1+ age-group		
	14	20	26	14	20	26
Catch	577	263	36	31	62	48
	692	251	28	35	81	73
	640	234		47	69	
		263			67	
Mean catch	636	253	32	38	70	61
% of age-group in stratum	69.1	27.5	3.5	22.5	41.4	36.1

The slope of the regression of survival on time was not significant in the absence of the above four points; thus the assumption of no measurable mortality is tenable.

Bartlett's test applied to the data in Table 3 indicated homogeneity of variances for the total estimates and for the age 0+ estimates ($X^2 = 5.42$ and 10.1; $0.5 < P < 0.1$) but heterogeneity for the age 1+ estimates ($X^2 = 19.6$; $.005 < P < .001$). Therefore, mean survival rate is probably a valid measure of survival for the age 0+ population during the sampling periods.

The necessity of complete supplementary townet data was demonstrated in the age 1+ estimates. In all years prior to 1974 the strategy was to set the townet at the depth containing the greatest concentration of fish targets. The resulting ratios of 0+ : 1+ fish were then taken, in the absence of any depth series data, to represent the proportion of each age-class within the population. That this method may have underestimated the numbers of age 1+ fish present, by assigning some of their numbers to the 0+ group, was apparent when the 1970 age 1+ inlake population was estimated at only 154 000 fish but returned 72 000 adults in 1973 and 1974. The data collected at the outlet weir on migrating smolts also consistently indicated a higher proportion of the older age-group than was apparent from the inlake estimates. This is expected to the degree that some of the younger age-group do not emigrate after their 1st yr in the lake, but the ratios varied in direct proportion to the relative strength of the age 0+ population. The heterogeneity of the age 1+ estimates was a further indication of some inconsistency in the sampling of this age-group.

In 1974 a depth series was incorporated into each townetting series, one of the purposes of which was to investigate the distribution with depth of the two major age-groups. The data from these series indicated a deeper distribution at some times for the age 1+ fish relative to the age 0+ fish. For instance, of the three depths containing significant target numbers on September 18, 62% of the total population sampled was represented in the most shallow tow. This included 69% of the age 0+ population but only 22% of the age 1+ population (Table 5). By contrast, the deepest tow contained only 8.5% of the total population, but included 36% of the age 1+ population. The ratio of the numbers of each age-group present in the shallow tow was 0.944 0+ to 0.056 1+. A population estimate using only this proportion, while slightly overestimating the 0+ present, would have indicated the numbers of age 1+ to be about 36% of those as calculated from the total series. This phenomenon became less evident and eventually disappeared as the fish assumed their winter distribution pattern and indeed reversed itself in the early spring preparatory to smolt emigration.

The variation of the expression of the phenomenon in proportion to the relative population sizes of the two age-groups is expected from the strategy of fishing at the depth of maximum concentration. This has an overall effect of minimizing the overestimation of the age 0+ proportion of the total population in any year. It also implies that the smaller the relative size of the age 1+ population, the more will its absolute number be underestimated. Within any year, the depth dispersion of the population varies seasonally. This would induce further variance into the age 1+ estimates, as seasonal sampling was not constant between years. The result of the combined effect of these two variables was the observed heterogeneity of sample means for the age 1+ sockeye estimates.

Bias in the experimental design prior to 1974 tended to underestimate the numbers of age 1+ fish present within the lake, because some age 1+ fish would be assigned to the 0+ population. Due to the dominance of numbers of age 0+ sockeye and the sampling strategy, this would contribute substantially to the observed variance in the 1+ estimates while having little effect on the 0+ estimates.

DEGREE OF ENHANCEMENT OF AGE 0+ SOCKEYE SURVIVAL

Mean annual survival of age 0+ sockeye from potential egg deposition was enhanced by at least 2.5 during years of fertilization relative to years of no fertilization (Table 4). A single classification analysis of variance on individual survival rates, with partitioning into between and among treatment components, gave the following results:

Source of variation	df	Mean square
Among years	7	56.1***
Unfertilized vs. fertilized	1	350.2***
Among unfertilized	3	12.7***
Among fertilized	3	1.39n.s.
Within years (error)	19	0.974

The greatest difference in the among years components is that between treatments. A highly significant difference is revealed in the among unfertilized years

component also, while no significant difference occurred among fertilized years.

The difference in unfertilized years is caused by 2 yr of relatively high survival paired with two of relatively low survival (Table 4). The pattern of growth of the age 0+ fish that survived at 6.13% in 1974 was more comparable to that in a fertilized year than to an unfertilized year (Robinson and Barraclough 1975b). In combination with the large number of fish in the lake that year, this resulted in the largest production of sockeye biomass observed during the experiment. By 1975 and 1976 the pattern of growth had returned to one comparable with the prefertilization year of 1969 (Barraclough and Robinson 1972).

The above indicates a carry-over of the effects of fertilization into 1974. This year is consequently suspect for evaluation purposes. It is suggested that this large number of fish imposed a cyclic pattern of survival on the succeeding year-classes by suppressing growth, and hence survival, of the fry emerging in the spring of 1975 through competition for food. The fry in 1976 had very little competition from older sockeye (Table 3) and this was reflected in a survival rate more than double that of the previous year. It is further suggested that the "steady state" survival rate in the absence of fertilization is intermediate between the 2.73 and 6.29% observed in 1975 and 1976, respectively, and that the apparent degree of survival enhancement of 2.5 is a conservative estimate of that attained.

General Discussion

The mean survival to the fall of the year during years of fertilization of 11.65% represents about 350 fry per female spawning in Great Central Lake. The range during unfertilized years of 2.73–6.29% represents about 82–189 fry per female. This is only a minor overestimate of smolts produced per female because of the subsequent low inlake mortality (see below).

Data from some Alaska lakes suggest that total survival there is low. The Ugashik Lake system yields an average of 22.4 smolts per female (Siedelman 1969), while Naknek Lake system averages 14.2 (Van Valin 1969). Data from Frazer Lake for the brood years 1963 and 1964 indicate total smolt production of 24.3 and 18.5 per female, respectively (Russell 1972). Data from some British Columbia lakes indicate more varied but generally higher survivorship. Cultus Lake produced a 9-yr average of 127 smolts per female, ranging from a low of 37 to highs of 237 and 306 in years of predator control (Foerster 1968, table 82). Production in coastal Port John Lake averaged 72 smolts per female between 1948 and 1955 (Foerster 1968, table 83) while Chilko Lake averaged 114 between 1949 and 1955 (Foerster 1968, table 86). More northerly Babine Lake averaged 130 for the brood years 1961 to 1971, with a range increasing from about 30 to 218 coincident with spawning channel developments (H. W. D. Smith, Pacific Biological Station, Nanaimo, B.C., personal communication).

Natural survival in Great Central Lake falls within the range observed for other British Columbia lakes. Survival during fertilization, however, is among the highest recorded for North American sockeye lakes.

A major factor affecting inlake survival appears to be predation. Removal of the predators from Cultus Lake resulted in much higher survival of juvenile sockeye. Predators have been found to cause significant smolt mortalities in some Alaska lakes (Rogers et al. 1972), and their role in establishing and maintaining cyclic dominance within the Fraser River system has been hypothesized (Ward and Larkin 1964).

The effect of predators on the survival of sockeye in Great Central Lake is thought to be small. Sockeye yearlings are a major component in the diet of the coastal cutthroat trout (*Salmo clarki clarki*) at some times of the year (Narver 1975), but these trout are few in absolute numbers, and are probably limited by the paucity of their juvenile rearing streams. The largest of the residual sockeye have been noted to take underyearlings occasionally, but again the number of these predators is small. Juvenile coho (*Oncorhynchus kisutch*) are numerous around the shores of the lake; they have been noted to prey heavily upon the eggs during spawning (Robinson and Barraclough unpublished data) but never upon underyearling sockeye (Mason 1974). These data apply to inlake fish to the fall of their underyearling year and some further losses do occur during smolt migration to cutthroat trout and to the larger of the coho smolts within the lake (Robinson and Barraclough unpublished data). The general indication is that predation rates were low and, combined with the inherent stability of a beach spawning system, result in consistent and relatively high natural survival of juvenile sockeye.

In conclusion, the acoustic counting–townet technique appears to provide reliable data from which to estimate the size and structure of lake sockeye populations. It is clear that a thorough knowledge of their seasonal behavior and distribution is essential for efficient sample design and data interpretation. It has been clearly demonstrated that fertilization benefited the survival of young sockeye salmon in Great Central Lake. The method developed to make this assessment provides a relatively efficient and accurate means of evaluating the juvenile populations upon which are based the subsequent adult returns to the commercial fishery.

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Fate of ^{14}C-benzene in Eggs and Larvae of Pacific Herring (*Clupea harengus pallasi*)

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Eggs and larvae of Pacific herring were exposed to low concentrations of ^{14}C-labeled benzene, a soluble, aromatic component of crude oil. All life stages accumulated benzene from water in direct proportion to the initial exposure concentrations, reaching equilibrium within 6–12 h. Feeding larvae exposed to benzene through water and live food accumulated benzene initially from the water, then secondarily from the food. The maximum amount of benzene accumulated in tissues was inversely related to age. Eggs accumulated up to 10.9 times the initial concentration, yolk-sac larvae up to 6.9 times, and feeding larvae to 3.9 times. Reasons for these differences in total accumulation and uptake rate are discussed. Results provide evidence for food web magnification of petroleum-based hydrocarbons.

Key words: Pacific herring, *Clupea harengus pallasi*, eggs and larvae, ^{14}C-benzene, uptake, depuration, food chain, petroleum-based hydrocarbons

ELDRIDGE, M. B., T. ECHEVERRIA, AND S. KORN. 1978. Fate of ^{14}C-benzene in eggs and larvae of Pacific herring (*Clupea harengus pallasi*). J. Fish. Res. Board Can. 35: 861–865.

Des oeufs et des larves de hareng du Pacifique furent exposés à de faibles concentrations de benzène, un constituant aromatique soluble du pétrole brut, marqué au ^{14}C. Tous les stades biologiques accumulent du benzène en provenance de l'eau en proportion directe des concentrations initiales d'exposition, jusqu'à ce qu'un équilibre s'établisse en dedans de 6 à 12 h. Des larves capables de se nourrir, exposées à du benzène à la fois dans l'eau et dans leur nourriture vivante, accumulent le benzène d'abord de l'eau, ensuite de la nourriture. La quantité maximale de benzène accumulée dans les tissus est en relation inverse de l'âge. Les oeufs accumulent jusqu'à 10.9 fois la concentration initiale, les larves vésiculées jusqu'à 6.9 fois et les larves qui se nourrissent jusqu'à 3.9 fois. Nous analysons les raisons de ces différences dans l'accumulation totale et le taux d'assimilation. Ces résultats sont une preuve de l'accroissement, dans le réseau alimentaire, des hydrocarbures du pétrole.

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NUMEROUS researchers have shown that marine organisms representing different species and trophic levels take up and release petroleum hydrocarbons (Lee et al. 1972; Teal and Stegeman 1973; Vaughan 1973; Anderson et al. 1974; Fossato 1975; Lee 1975; Corner et al. 1976; Korn et al. 1976). In radiometric studies marine organisms more rapidly metabolized *n*-alkanes than aromatics (Lee 1975).

Studies of the relatively more toxic aromatic fractions have concentrated on the higher aromatics and only lately have investigators examined benzene, a relatively abundant (up to 6.75 mg/L in the water-soluble fraction) and soluble aromatic (1993 μL/L) component of crude oil (Anderson et al. 1974; Benville and Korn 1974). Benzene at concentrations of 20–45 μL/L is acutely toxic and at 5–10 μL/L is chronically toxic to Pacific herring (*Clupea harengus pallasi*) eggs and larvae (Struhsaker et al. 1974) and at 2–11 μL/L is acutely toxic to various juvenile and adult fishes (Meyerhoff 1975; Benville and Korn 1977). Korn et al. (1976, 1977) and Roubal et al. (1977) found that in juvenile and adult fishes aqueous benzene rapidly entered the fish and was metabolized in the liver. In nearly all studies

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TABLE 1. Summary of experimental variables for ^{14}C-benzene uptake and depuration tests with Pacific herring embryos and larvae. All tissues were sampled at 6, 12, 24, 48, and 72 h except marked (*) treatments, which ended at 48 h.

Life stage	Type of exposure	Initial mean benzene concn (μL/L)	Specific activity (cpm/nL)	Total wet wt (mg) mean	±SD	Estimated no. of individuals per sample
Egg—embryo	Benzene-treated water	0.063	20.00	158.9	±21.3	81
		0.560	2.00	155.3	±16.0	79
Yolk-sac larva	Benzene-treated water	0.036	13.00	147.2	±56.2	118
		0.460	0.90	127.9	±46.6	102
Postyolk-sac larva	Benzene-treated water	0.144	2.20	154.5	±35.5	144
		1.200*	5.00	135.1	±36.1	126
		2.100	0.14	170.4	±40.4	158
	Benzene-treated food and clean water	1.200*	5.00	117.5	±25.6	109
	Benzene-treated water and clean food	1.440*	2.20	149.7	±70.1	139
		2.100	0.14	148.8	±65.7	138
	Benzene-treated food and water	1.200*	5.00	129.2	±43.1	120

juvenile and/or adult life stages were used, and they were only exposed to hydrocarbons in the water.

The object of this study was to determine the fate of benzene in the eggs, yolk-sac larvae, and feeding larvae of Pacific herring. We wished to compare the uptake of benzene from the water with that from food and determine whether biomagnification occurred, as has been demonstrated with pesticides (Hickey and Keith 1965; Woodwell et al. 1967; Macek and Korn 1970; Reinert 1972).

Materials and Methods

Test Animals

For experiments with eggs, Pacific herring (*Clupea harengus pallasi*) eggs were artificially fertilized with gametes of freshly caught, sexually mature adults. A single layer of eggs was spread over 10 × 24 cm glass plates and placed in green polyethylene-plastic rectangular pans filled with 8 L of filtered (pore size 2 μm) seawater. In the experiments with larvae, naturally fertilized eggs were gathered in San Francisco Bay and incubated in similar pans. After hatching, larvae were transferred to new pans filled with freshly filtered seawater.

Postyolk-sac feeding larvae (9.4 mm mean standard length) were fed marine rotifers (*Brachionus plicatilis*) which were cultured according to the techniques of Theilacker and McMaster (1971), except that the small green flagellate (*Nephroselmis* sp.) was used as rotifer food. Rotifer concentrations were maintained at 14–20 rotifers/mL as determined with a Model ZBI Coulter counter.

Experimental Conditions

Experiments were conducted in the previously described 8-L pans, under static conditions. Freshly filtered seawater was added at the beginning of each experiment, and temperature, dissolved oxygen, and salinity were measured daily. To stabilize water conditions pans were held in water baths under constant light (about 1900 lx). Dissolved oxygen values were at or near saturation, salinities were constant at 23.0‰, and temperature ranged from 12.2 to 13.5°C throughout the experiments.

Exposure Procedures

Animals were given a single dose of benzene just after fertilization, just after hatching (yolk-sac larvae), and at completion of yolk absorption (feeding larvae). They were therefore exposed to continuously declining concentrations of benzene, which from previous experiments has been shown to decline exponentially to ~25–30% of the initial concentration within 24 h (Struhsaker et al. 1974). Aqueous benzene was introduced directly into the water in the form of benzene-saturated seawater (1 mL benzene to 250 mL seawater vigorously shaken and settled for 1 h). Ring-labeled ^{14}C-benzene of the desired specific activity (Table 1) was added to this stock solution and the appropriate amount of benzene added to the test containers. An attempt was made to introduce benzene in two concentrations of 1.00 and 0.10 μL/L. Due to its volatility and the difficulty in dissolving benzene, the actual in situ concentrations of benzene ranged from 0.010 to 2.100 μL/L as determined by gas chromatography (Table 1). In the feeding larval experiment ^{14}C-labeled benzene was introduced in three ways: (a) in contaminated water only, without food, (b) in benzene-contaminated rotifers only, and (c) in benzene-contaminated water and benzene-contaminated rotifers.

We contaminated the rotifers by introducing ^{14}C-labeled benzene to the rotifer rearing container at ~0.1 and 1.0 μL/L concentrations. The rotifers were allowed to accumulate benzene for 2 d. They were then removed, rinsed with fresh seawater, and fed to the larvae.

Water and Tissue Analyses

Two water and tissue samples were taken at 6-, 12-, 24-, 48-, and 72-h intervals. The 1-mL water samples were added to 10 mL Instagel scintillator and counted in a Packard Tri Carb scintillation spectrometer. For tissue samples live larvae were rinsed with distilled water, weighed (Table 1), placed in a vial with solubilizing solution (1 mL/100 mg tissue Packard Soluene-100) for 48 h and combined with 10 mL of scintillator (Packard Dimilume). To avoid rapid drying of the samples and the potential loss of benzene we

TABLE 2. Decreasing concentrations (μL/L) over 48 h of ^{14}C-labeled benzene in the water of experiments with Pacific herring eggs and larvae.

Expt	Life stage	Hours					% volatilized at 24 h
		0	6	12	24	48	
1	Embryo	0.063	0.007	0.007	0.003	—[a]	60
1	Embryo	0.560	0.035	0.029	0.023	—	77
2	Yolk-sac larva	0.036	0.023	0.020	0.018	—	50
2	Yolk-sac larva	0.460	0.356	0.329	0.205	—	55
3	Postyolk-sac larva	0.144	0.088	—	0.056	—	61
3	Postyolk-sac larva	2.100	1.320	—	0.723	—	68
4	Postyolk-sac larva	1.200	0.800	0.580	0.360	—	60

[a]No detectable concentration.

did not count the numbers of individuals in each sample. Rather, we estimated their numbers (Table 1) by using Ehrlich's (1972) determinations of water content and our own dry weight measurements. Method efficiency was 61%, predetermined with spiked samples of known counts per minute (cpm). Water and tissue samples with emissions below 40 cpm were considered below the detectable limits of our system.

Radiometric analysis measures ^{14}C and cannot determine if the label remains on an intact benzene ring or on a metabolite of benzene. Since we did not analyze for the presence of benzene metabolites, all results and discussion on accumulation and depuration must be considered to represent benzene and/or benzene metabolites.

Results and Discussion

Aqueous benzene concentrations in our test containers decreased exponentially in the first 24 h after introduction (Table 2) as was found in previous larval fish experiments (Struhsaker et al. 1974); benzene was absent after 48 h.

Embryos and yolk-sac larvae responded to single exposures of aqueous benzene in almost identical fashion. Both rapidly accumulated benzene to maximum levels within 6–12 h after exposure (Table 3). Embryos then lost benzene at an exponential rate, declining to levels just above the initial exposure concentrations. Yolk-sac larvae began depurating between 24 and 48 h but differed from embryos by exhibiting an increase in ^{14}C-benzene between 48 and 72 h. How yolk-sac larvae accumulated benzene after a period of depuration is difficult to explain, since free benzene was not detectable in the water. However, fish larvae are known to increase their tissue water content when starved (Ehrlich 1974). Until feeding is well established some tissue resorption takes place, a condition which, if continued, would lead to starvation and eventual death. Benzene may enter larvae via infused water.

Like embryos and yolk-sac larvae, nonfeeding postyolk-sac larvae exposed to three aqueous concentrations (0.144, 1.200, and 2.100 μL/L) quickly absorbed benzene, attaining maximum accumulations within 6–12 h (Table 3). Subsequent depuration followed with leveling off at or near the original exposure concentrations.

Postyolk-sac larvae feeding on contaminated rotifers or rotifers in contaminated water demonstrated a bimodal uptake response to benzene exposure. When benzene in situ concentrations of 0.140 and 2.100 μL/g were added to water containing larvae actively feeding on clean rotifers, larvae rapidly accumulated benzene during the first 6 h (Table 3). This initial accumulation was similar to the previously described response of unfed larvae and presumably represents uptake of aqueous benzene. Depuration from larval tissues between 6 and 24 h was slow or nonexistent, and after this period uptake was again exhibited. Maximum concentrations of 0.49 and 8.160 μL/g were reached at 48 and 72 h for the low and high exposure concentrations, respectively. Larvae apparently ingested rotifers during this latter period which had become contaminated from the aqueous benzene. In a separate treatment larvae exposed to both contaminated water and precontaminated rotifers responded the same as larvae exposed to benzene-contaminated water only and clean rotifers (the 0.140 and 2.100 μL/L of Table 3). The initial benzene accumulation in the doubly exposed larvae reached 2.47 and the second buildup reached 3.98 μL/L. In the final treatment, larvae that fed on only rotifers previously contaminated with 1.200 μL/L benzene experienced no initial rapid accumulation; rather a steady rise in contamination to 0.310 μL/L was exhibited.

The secondary accumulation of benzene by ingestion of rotifers appeared to be a lower but potentially more accumulative process. The principal reason for this is that *B. plicatilis* appears incapable of either discharging or metabolizing benzene for time periods far exceeding the developmental period when herring larvae would depend on them for food (Echeverria unpublished data). In experiments conducted at our laboratory we found rotifers accumulated and retained benzene and/or its metabolites 10^3–10^4 times the original concentration for periods up to 8 d. Larvae fed on rotifers that in turn were accumulating higher concentrations of ^{14}C hydrocarbons. The longer time period needed for rotifers to

TABLE 3. Means ±SE of benzene concentrations (nL/g) in exposed Pacific herring eggs and larvae.

Life stage	Initial exposure concn (μL/L)	Hours				
		6	12	24	48	72
Embryo	0.063	0.58±0.04	0.61±0.01	0.32±0.02	0.18±0.01	0.10±0.00
	0.560	6.10±0.30	6.14±0.19	3.45±0.14	1.26±0.02	0.91±0.00[a]
Yolk-sac larva	0.036	0.25±0.01	0.13±0.02	0.09±0.01	0.10±0.00	0.39±0.01
	0.460	2.40±0.15	3.12±0.19	1.81±0.10	0.67±0.02	0.89±0.02
Unfed larva	0.144	0.22±0.02	0.23±0.02	0.17±0.01	0.18±0.03	0.17±0.00[a]
	1.200	3.21±0.00[a]	3.10±0.09	1.44±0.09	1.24±0.21	—
	2.100	4.09±0.09	4.06±0.09	2.84±0.19	2.78±0.02	2.74±0.05
Fed larva	0.140	0.23±0.01	0.25±0.01	0.26±0.00	0.49±0.07	—
	1.200	0.04±0.01	0.10±0.05	0.22±0.07	0.31±0.04	—
	1.200	2.47±0.04	2.28±0.04	1.78±0.04	3.98±0.00[a]	—
	2.100	4.99±0.04	4.23±0.03	3.27±0.05	6.22±0.12	8.16±0.15

[a]Only one sample used for calculation.

take up and concentrate these hydrocarbons explains the secondary or delayed response in herring uptake. The presence of aqueous benzene seems to affect the amount of benzene taken up by rotifers and hence by larvae. When contaminated rotifers alone were present, larvae accumulated only 0.3 μL/L of the original concentration. Further sampling beyond 48 h is needed to determine whether larvae would continue to accumulate benzene. In a simple comparison between results (Table 3), we calculated the relative contribution of benzene derived from the water versus from the food. In the first rapid uptake an average of 91% of tissue benzene was obtained from the water. The second peak at 48 h was an average of 38% from the water and 62% from rotifers. Presumably larvae would proportionally take up more benzene from rotifers in time as waterborne benzene concentrations declined and rotifers accumulated more.

The maximum amount of benzene accumulated in tissues differed among early life stages. The younger the stage, the higher the concentration factor. Eggs absorbed benzene 9.7 and 10.9 times the concentrations added to the water, and yolk-sac larvae accumulated 6.9 and 6.8 times the initial concentration. After yolk absorption, larvae accumulated less benzene than either eggs or yolk-sac larvae. Factors ranged from 0.3 for larvae feeding on precontaminated rotifers to 3.9 times the initial exposure concentration in larvae feeding on rotifers in benzene-contaminated water. This highest accumulation of benzene occurred 72 h after exposure (Table 3) when larvae were feeding on rotifers and there was no indication of a decrease in accumulation. The uptake patterns seen in the accumulations of other postyolk-sac larvae fed rotifers (Table 3) also suggest maximum levels had not been reached. No samples were taken after 72 h.

All stages accumulated benzene rapidly from the water, but those with yolk exhibited higher tissue magnification factors than larvae past the stage of yolk absorption. Higher concentration factors in these yolk-containing stages are most likely caused by two factors: the high lipid content of yolk-bearing stages and the lack of specialized tissues. Korn et al. (1976) found benzene accumulated predominantly in tissues with high lipid content in teleosts. Lipophilic benzene probably accumulated in the lipid-rich yolk of the herring eggs and yolk-sac larvae. The content of lipids in conspecific Atlantic herring (*Clupea harengus harengus*) eggs has been determined by Ehrlich (1972) to be 18.12% of egg dry weight. In related experiments we measured oxygen consumption which showed herring larvae had much higher metabolic rates than eggs. This would mean utilization of lipid-rich yolk and excretion rates would be less in embryos than in active larvae, thereby affecting the turnover rate of benzene in the two life stages.

It is commonly believed the liver is a major site of petroleum hydrocarbon metabolism. Livers and gallbladders of adult fishes have been found to accumulate the highest concentrations of benzene over all tissues tested (Korn et al. 1976; Roubal et al. 1977). The metabolism and/or depuration of benzene is likely slower in the less-developed life stages lacking these functional organs.

Until recently no evidence existed for food-web magnification of petroleum-based hydrocarbons (Lu and Metcalf 1975; National Academy of Sciences 1975; Koons et al. 1976). Corner et al. (1976), however, found that *Calanus helgolandicus* responded to naphthalene exposure in much the same manner as did herring larvae. Hydrocarbons accumulated through the diet were quantitatively more important than those taken up directly from solution. Accumulation and depuration of hydrocarbons were much slower when obtained from contaminated food. Results of our study clearly demonstrated that fish larvae feeding on zooplankters that cannot metabolize or discharge petro-

leum hydrocarbons in short time periods do accumulate hydrocarbons to amounts in excess of the exposure concentrations. Further, zooplankters of this type or copepods with high hydrocarbon contents provide a pathway of entry for petroleum hydrocarbons that may be more significant than through the water.

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Water Temperature Fluctuations and Seasonal Periodicity of *Cladophora* and *Potamogeton* in Shallow Rivers

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WONG, S. L., B. CLARK, M. KIRBY, AND R. F. KOSCIUW. 1978. Water temperature fluctuations and seasonal periodicity of *Cladophora* and *Potamogeton* in shallow rivers. J. Fish. Res. Board Can. 35: 866–870.

The influence of water temperature on nuisance plant species in seven river systems in southwestern Ontario was investigated. Nutrients were not limiting. The study period covered the low flow season from May to September, 1973–76. A community dominated by *Cladophora glomerata* in late spring is usually replaced by a *Potamogeton pectinatus* dominated community. The tolerance limits of *C. glomerata* and *P. pectinatus* at fixed values of the daily mean or daily maximum temperature change with the daily temperature range. Two methods of predicting daily range were derived. An intermediate seasonal temperature (18–22°C, <4°C daily temperature fluctuation) supported a mixed plant community. Maintenance of appropriate temperature conditions could provide a management technique for controlling nuisance plant growths or for establishing a diverse community in shallow rivers.

Key words: Potamogeton, Cladophora, temperature, seasonal periodicity, rivers

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Les auteurs ont étudié l'influence de la température de l'eau sur certaines pestes végétales dans sept réseaux fluviaux du sud-ouest de l'Ontario. Les éléments nutritifs n'étaient pas un facteur limitatif. La période d'étude couvrit la saison d'étiage de mai à septembre 1973–76. Une communauté dominée par *Cladophora glomerata* tard au printemps est ordinairement remplacée par une communauté dominée par *Potamogeton pectinatus*. Les limites de tolérance de *C. glomerata* et de *P. pectinatus* à des valeurs fixes de la moyenne quotidienne ou du maximum quotidien de température changent en fonction de la gamme quotidienne de températures. Nous avons établi deux méthodes de prédiction de la gamme quotidienne. Une température saisonnière intermédiaire (18–22°C, fluctuation quotidienne de température de <4°C) supporte une communauté végétale mixte. Le maintien de températures appropriées pourrait fournir une technique de gestion permettant de contrôler la croissance des plantes nuisibles ou d'établir une communauté diversifiée dans les rivières peu profondes.

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FACTORS affecting plant growth are of considerable importance in the field of river management. If accurate data concerning the environmental requirements of aquatic species were available they could provide a sound basis for the development of guidelines for controlling nuisance aquatic vegetation. We attempted to correlate the effects of water temperature and the seasonal pattern of species distribution and abundance in seven river systems in southwestern Ontario.

The most common plant species in the study areas are *Cladophora glomerata* and *Potamogeton pectinatus* (Wong and Clark 1976). *Cladophora glomerata* exhibits a short period of intensive vegetative growth in May or June and another in September or October. The second period of growth yields less total biomass than the first. Short tufts of healthy *Cladophora* are often left at the time of freeze-up. *Potamogeton pectinatus* is usually dominant between the two pulses of *Cladophora*. Although the factors responsible for such seasonal sequences of plant communities are not definitely known (Storr and Sweeney 1971), it has been suggested that temperature plays an important role, particularly in areas where nutrients are readily available (Bellis and McLarty 1967). This hypothesis is supported by the observation that aquatic species have characteristic thermal requirements (Patrick 1968; Sculthorpe 1971). Water temperature is also important for management purposes, since it could be more readily controlled than most environmental variables. Rivers having high back-

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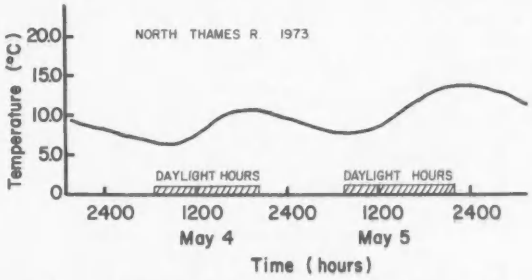

FIG. 1. Daily fluctuations of temperature for the North Thames River on May 4 and 5, 1973. Daylight hours are shown in relation to temperature.

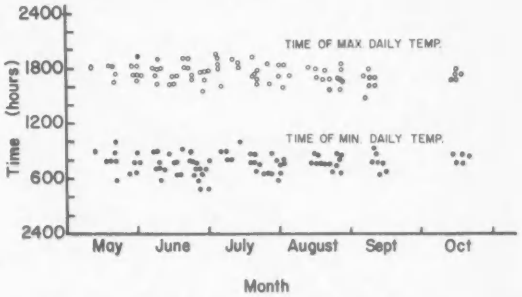

FIG. 2. Hour of daily maximum and minimum temperatures for randomly selected temperature curves from eight river sections in southwestern Ontario 1973–76. Open circles represent the time of maximum temperature and closed circles the minimum.

ground nutrient levels from diffuse sources and large areas of substrate suitable for colonization of aquatic plants are difficult to manage by nutrient removal alone. The maintenance of desirable water temperatures in combination with nutrient removal may help avoid nuisance growths of highly productive species. Consequently, the scope of this report is restricted to studying the effect of water temperature on the seasonal periodicity of *Cladophora* and *Potamogeton*.

It is difficult to isolate the effects of water temperature on the life cycles of aquatic plants from the effects of other growth-controlling factors that operate simultaneously and interact in complex ways. Traditionally, thermal requirements have been investigated under controlled laboratory conditions, but to date such studies have placed little emphasis on the effect of diurnal temperature fluctuations. The growth response of aquatic plant species to thermal fluctuations is not well documented (Wurtz 1968), but the large body of evidence attesting to the importance of its influence on fish populations leaves little doubt that it should not be ignored (Hokanson et al. 1977). Moreover, the reported thermal tolerance levels of some species, e.g. *Cladophora* sp. (Whitton 1970), cover a considerable range.

The approach adopted here is potentially valuable to river managers because temperature effects were investigated in the field and because the influence of diurnal temperature changes (including range of fluctuations) were considered.

Materials and Methods

Field investigations were conducted during the low flow season (May–September), 1973–76. Eight river sections were selected on the basis of similarity of substrate and uniformity of river depth from seven river systems in southwestern Ontario: the Avon, Conestogo, Middle Maitland, Nith, Speed, Thames, and Grand (Wong and Clark 1976). The study areas have minimal groundwater and tributary inflow, a substrate of coarse rubble, and mean depths of ~0.3–0.6 m during low flow conditions. Nutrients were not limiting (Wong and Clark 1976; Painter et al. 1976).

Diurnal fluctuations in water temperature were recorded continuously with temperature compensator/resistance thermometers attached to E.I.L. oxygen meters (Electronic Instruments Ltd., Richmond, Surrey, England), coupled with Rustrak recorders (Gulton Industries, Manchester, N.H.). Solar radiation was recorded with a Weather Measure R401 Pyranometer (Weather Measure Corporation, Sacramento, Calif.). Daily photoperiod was determined from solar radiation charts.

Plant communities were sampled at 1–3 wk intervals throughout the summer, with more intensive sampling during periods of transition. Visual estimates of the percentage abundance of each species were obtained from harvested material, quadrat photographs, and drifting plant material collected on wire screens installed in midstream of the main channel. A species was considered dominant during a particular time interval if its abundance was >70% of total biomass.

Results and Discussion

General Aspects of Water Temperature

A representative graph of the changes in water temperature over 2½ d is presented in Fig. 1. The occurrence of temperature increases during daylight hours supports the hypothesis of a relationship between the rate of temperature increase and the rate of solar energy input.

The daily minimum and maximum temperatures occur at ~0730 and 1800 h, respectively, each day throughout the summer (Fig. 2). Since the time interval between the maximum and minimum temperatures is constant and roughly corresponds to day length, the temperature range is directly proportional to the rate of change in the water temperature during daylight hours.

Regression analysis of daily range of water temperature and rate of solar radiation input for each month of the low flow season are shown in Fig. 3. The correlation coefficients (r) range from 0.61 (for August) to 0.75 (for July). The lines are roughly parallel, but differ in their intercepts on the water temperature fluctuation axis. July has the lowest intercept, suggesting that radiation input in July must be higher than in any other month if a constant temperature range were

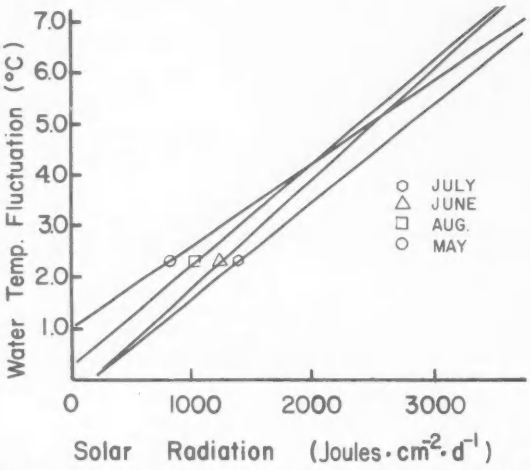

FIG. 3. Relationship between solar radiation and daily water temperature fluctuation for May–August in eight river sections in southwestern Ontario.

to be maintained throughout the low flow season. This is a consequence of differences in the rate of heat dissipation by evaporation associated with differences in day-length rhythms (Krenkel and Parker 1968).

The slopes of the lines were tested for homogeneity yielding an F value of 0.082 with 3 and 73 degrees of freedom. The differences were not significant ($P = 0.100$). This implies that changes in evaporation, advection and conduction are relatively small throughout the summer.

The following general relationship between range in daily temperatures and rate of solar radiation input was obtained by pooling all the data:

$$\Delta T = 0.081 + 0.002\, I_0 \; (r = 0.71), \tag{1}$$

where ΔT is the range of daily water temperature and I_0 is the light energy input in joules per square centimetre per day. This equation may be used to obtain a rough estimate of the range of daily water temperature from the daily light energy input, as long as there are no waste-heat disposal sites upstream.

For water temperatures that follow a regular daily pattern, the daily range is governed by other temperature aspects, such as the maximum, minimum, and mean temperatures, and by the coefficient of heat exchange between the air and water. When the daily mean and daily maximum are emphasized, the daily temperature range can be expressed as

$$\Delta T = f(\bar{T}, T_{\max}),$$

where ΔT is the daily temperature range, $T_{\max}$ is the daily maximum temperature, and $\bar{T}$ is the daily mean temperature obtained by integrating the temperature over a 1-d period and dividing by 24.

Diurnal water temperature curves were compiled

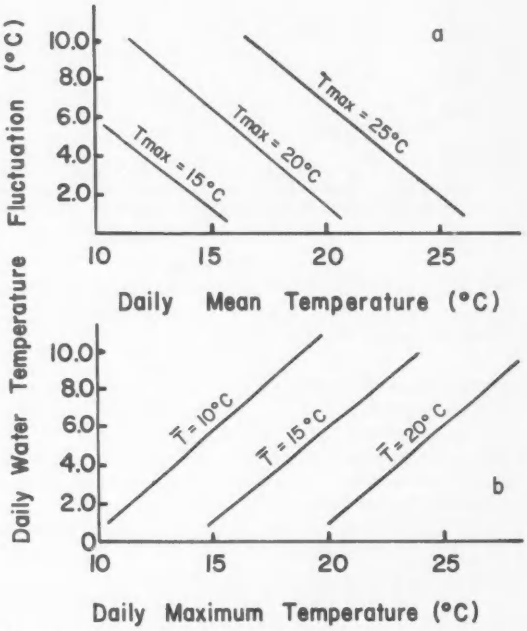

FIG. 4. Relationship between daily water temperature fluctuation and (a) daily mean temperature for $T_{\max}$ values of 15, 20, and 25°C and (b) daily maximum temperature for mean temperature values of 10, 15, and 20°C.

from various river sections. The following multiple regression equation was calculated with 168 complete sets:

$$\Delta T = 0.22 + 1.02\, T_{\max} - 0.96\, \bar{T} \; (r = 0.805).$$

Graphs of the partial regression of water temperature range with daily mean and daily maximum are presented in Fig. 4.

On the basis of the above relationship, a simple field measurement of water temperature during its peak (1700–1900 h) would be sufficient to estimate the daily range of water temperature from equation (2). The required value of mean daily water temperature can be estimated from the mean air temperature (Song and Chien 1977).

Effect of Water Temperature on Seasonal Plant Growth

Monthly and annual means of daily water temperature can provide information on general trends in the seasonal distribution of aquatic species, but are not sensitive enough to correlate with patterns of species dominance and degeneration, or community succession. This is a consequence of the extreme sensitivity of aquatic plants to short-term environmental exposures. For example, the filamentous alga, *Cladophora*, has been observed to develop to a great length in a matter

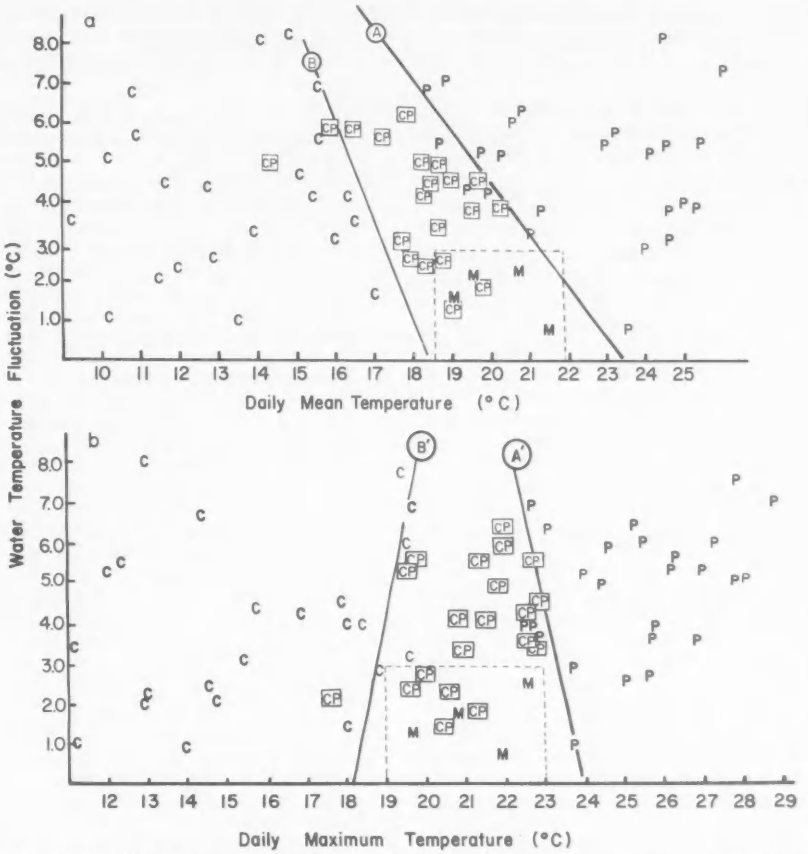

FIG. 5a, b. Occurrence of *Cladophora glomerata*, *Potamogeton pectinatus*, and mixed species in relation to water temperature in eight river sections in southwestern Ontario. C = *Cladophora glomerata* dominance, P = *Potamogeton pectinatus* dominance, CP = co-dominance of *C. glomerata* and *P. pectinatus*, and M = mixed community of *Cladophora*, *Potamogeton*, *Myriophyllum*, *Valisneria*, *Ceratophyllum*, and *Ranunculus*. Lines A and A′ delineate upper tolerance limit of *C. glomerata*, and lines B and B′ lower tolerance limit of *P. pectinatus*. Broken lines forming a rectangle approximate tolerance limits of the mixed plant community.

of days. It is, therefore, important to trace community growth on a daily basis. By identifying the dominant plant species and the corresponding temperature conditions, the significance of day-to-day water temperature variations can be compared with long-term temperature effects.

Various components of daily water temperature along with the corresponding dominant plant species are presented in Fig. 5. *Cladophora glomerata* is dominant in the lower range of water temperature and *P. pectinatus*, in the higher range. At intermediate temperatures, a codominant or a mixed community is found.

The codominant plant community occurred during the short transitional period in May or June when *C. glomerata* is replaced by *P. pectinatus*. The mixed community was observed on rare occasions, such as in 1976, when the water temperature in the upper Grand River fluctuated about the midtemperature range throughout the summer season. In this case there was no distinct period of dominance by *P. pectinatus*. Other species such as *Myriophyllum*, *Valisneria*, *Ceratophyllum*, *Ranunculus*, and *Cladophora* were evident at this time.

TOLERANCE LIMITS OF *Cladophora glomerata* AND *Potamogeton pectinatus*

The tolerance limits of *C. glomerata* and *P. pectinatus* were visually determined by drawing lines A and B in Fig. 5a and lines A′ and B′ in Fig. 5b at the interfaces

of the transitional zone. These figures suggest that the tolerance limits of *Cladophora* and *Potamogeton* at a given value of mean or maximum temperature vary with daily range.

The upper tolerance limits of *C. glomerata* under constant water temperature conditions can be approximated by extrapolating lines A and A′ to the point of zero water temperature fluctuation. The tolerance limit for *Cladophora* (from Fig. 5) is 23.5°C. This agrees closely with the 24–25°C limit derived from laboratory findings (Whitton 1967). Similarly, the intercepts of lines B and B′ at 18°C represent the lower tolerance limit of *Potamogeton*, and coincide with the optimal temperature requirements of *Cladophora* reported in the literature (Bellis and McLarty 1967; Whitton 1970). However, zero water temperature fluctuations very seldom occur under natural conditions; thus biological temperature coefficients derived under laboratory conditions of constant temperature would have limited practical application.

Temperature regulation may provide a sound basis for controlling nuisance vegetation. On one occasion in 1973, the entire *Cladophora* population of the North Thames River disappeared in approximately 5 d. This was followed by a period lasting about 10 d during which no vegetation was evident in the river. A plant community dominated by *Potamogeton pectinatus* subsequently developed. A temperature effect is believed to be responsible for the rapid disappearance of the *Cladophora*, since nutrients and flow remained constant. The daily mean and maximum water temperatures recorded for 3 d during the no-vegetation period were 4–6°C higher than those recorded for the same time period in the following year, when the usual sequence of vegetation changes was observed. These temperatures were also similar to those that normally occur 3–4 wk later in the summer when the plant community is usually dominated by *Potamogeton pectinatus*.

The tolerance limits of the mixed plant community (Fig. 5) are 18.5–22.0°C (mean temperature) with <3°C daily fluctuation. These lie in the transitional zone between the *Cladophora* and *Potamogeton* dominated communities.

Patrick (1968) has suggested that the diversity of the plant community reflects the stability of a river ecosystem. If this is the case, maintenance of the above temperature conditions could lead to a reestablishment of a stable community in degraded streams.

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Hyperosmotic Infiltration: Factors Influencing Uptake of Bovine Serum Albumin by Rainbow Trout (*Salmo gairdneri*)

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FENDER, D. C., AND D. F. AMEND. 1978. Hyperosmotic infiltration: factors influencing uptake of bovine serum albumin by rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 35: 871–874.

Infiltration of bovine serum albumin (BSA) into the blood of rainbow trout (*Salmo gairdneri*) by hyperosmotic infiltration (HI) was studied by varying the osmotic pressure, immersion time, pH, temperature, stress, vacuum, and fish size. Compared with uptake of BSA from water solutions, about 1400 mosM (4.51%) NaCl was required to increase the plasma level of BSA during a 3-min immersion. Higher osmotic pressures resulted in higher plasma-BSA levels, but the uptake of BSA was limited by the length of time that fish could tolerate the high NaCl concentration. Comparison of immersion time in the solutions of the two-step HI method showed that maximum infiltration occurred after a 2–3-min bath in the 5.32% NaCl solution and only 30 s in the 2% BSA solution. Alkaline solution (pH 9) enhanced BSA uptake in the one-step method, but the two-step method was most effective if the NaCl solution was pH 9 and the BSA solution pH 5. BSA uptake was directly proportional to water temperature from 4 to 20°C. Preimmersion stress, and injection of 10 μg epinephrine, reduced BSA uptake; vacuum and fish weight (2–8 g) had no effect on uptake of BSA. Hyperosmotic infiltration may be useful for mass delivery of vaccines, pharmaceuticals, and other materials.

Key words: hyperosmotic infiltration, bovine serum albumin, osmotic pressure, vaccines, immersion, rocket immunoelectrophoresis

FENDER, D. C., AND D. F. AMEND. 1978. Hyperosmotic infiltration: factors influencing uptake of bovine serum albumin by rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 35: 871–874.

Nous avons étudié la pénétration d'albumine sérique bovine (BSA) dans le sang de la truite arc-en-ciel (*Salmo gairdneri*) par infiltration hyperosmotique (HI) en faisant varier la pression osmotique, la période d'immersion, le pH, la température, le stress, le vide et la taille des poissons. Comparativement à l'absorption de BSA à partir de solutions aqueuses, environ 1 400 mosM (4.51%) de NaCl est requis pour augmenter le niveau plasmique de la BSA durant une immersion de 3 min. Des pressions osmotiques plus élevées produisent de plus hauts niveaux de BSA plasmique, mais l'assimilation de la BSA est limitée par la période de temps durant laquelle le poisson peut tolérer la haute teneur en NaCl. Une comparaison de la durée d'immersion dans des solutions de la méthode HI en deux étapes démontre que le maximum d'infiltration a lieu après un bain de 2 à 3 min dans la solution de NaCl à 5.32% et après seulement 30 s dans la solution de BSA à 2%. Une solution alcaline (pH 9) favorise l'absorption de la BSA dans la méthode à une étape, mais la méthode à deux étapes est plus efficace si la solution de NaCl a un pH de 9 et la solution de BSA, un pH de 5. L'absorption de la BSA est directement proportionnelle à la température de l'eau dans les limites de 4 à 20°C. Le stress de préimmersion et l'injection de 10 μg d'épinéphrine diminuent l'absorption de la BSA; le vide et le poids du poisson (2 à 8 g) n'ont pas d'effet sur l'absorption de la BSA. L'infiltration hyperosmotique peut être utile dans l'administration en masse de vaccins, de matériaux pharmaceutiques ou autres.

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HYPEROSMOTIC infiltration (HI) was introduced as a method for delivering antigens and possibly other substances into fish by Amend and Fender (1976). Recently HI was shown to be effective in immunizing sockeye salmon (*Oncorhynchus nerka*) against *Vibrio anguillarum* (Croy and Amend 1977). Antipa and Amend (1977) used HI in the field for successful vaccination of coho (*O. kisutch*) and chinook salmon (*O. tshawytscha*) against vibriosis in commercial operations.

Amend and Fender (1976), who used bovine serum albumin (BSA) as a test antigen to simulate vaccine uptake after HI of rainbow trout (*Salmo gairdneri*), indicated that uptake was mostly through the lateral line and partly through the gills. Here we compare levels of plasma-BSA after HI in which we used various osmotic pressures, immersion times, pH levels, and water temperatures. Effects of stress, vacuum, and fish weight were also studied.

Materials and Methods

Rainbow trout (weight, 2–8 g) of the Kamloops strain were used in these studies. Using techniques previously described (Amend and Fender 1976; Fender 1976), we infiltrated fish with BSA by immersing them for 3 min in the one-step HI solution (5.32% NaCl plus 2% BSA), or by immersing them for 3 min in each solution of the two-step HI procedure (5.32% NaCl "priming" solution, followed by a 2% BSA solution). After immersion the fish were returned to flowing dechlorinated municipal water for 45 min, and then bled by severing the caudal penduncle. The plasma was quantitatively assayed for BSA content by rocket immunoelectrophoresis (Kenny and Foy 1975) from a minimum of five fish in each test group.

We evaluated the influence of external osmotic pressure on the appearance of BSA in the plasma by varying the NaCl concentrations from 0 to 1650 mosM in the one-step HI. The minimum immersion time in the BSA solution of the two-step HI to obtain maximum plasma BSA levels was tested by first priming fish in the NaCl solution for 3 min, then varying the length of immersion in the BSA solution from 0.5 to 12 min. The effect of temperature was evaluated by acclimating fish to 4, 10, 15, and 20°C, then immersing them for 3 min in the one-step HI at each temperature. Fish were separated into three groups averaging 2, 4, or 8 g, then were immersed for 3 min in the one-step HI to determine whether the uptake of BSA was influenced by fish weight.

We tested the effect of vacuum on BSA infiltration into fish from the one-step HI solution by using the standard 5.32% NaCl solution or an isosmotic 10% urea-BSA solution. Immediately after immersion, fish were subjected to reduced atmospheric pressure (250 mm Hg) in a desiccator evacuated by a vacuum pump (Amend 1976). The vacuum was maintained for 3 min before normal atmospheric pressure was reinstated. To evaluate the effect of vacuum alone, without the hyperosmotic influence, we carried out identical experiments using only a 2% BSA solution. Control fish were treated for 3 min in each of the test solutions without vacuum.

The effect of stress on BSA uptake was determined by either holding fish in a net out of water for 2 min and then subjecting them to HI 30 min later, or by injecting 10 μg epinephrine intraperitoneally (i.p.) into each fish and then subjecting them to HI about 10 min later. Controls included unstressed fish and fish injected i.p. with phosphate-buffered saline (PBS) at pH 7.2. Each group was immersed in the one-step HI for 3 min and sampled as described.

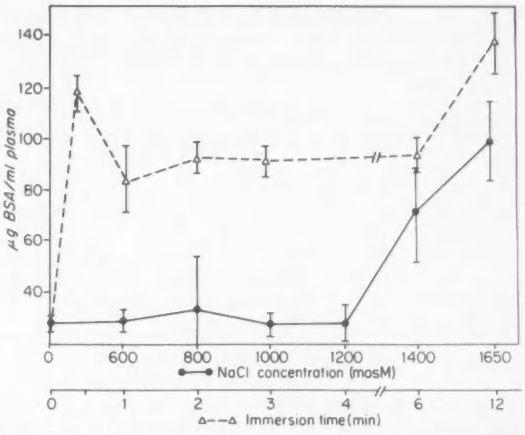

FIG. 1. Influence of NaCl concentration (mosM) on BSA infiltration from the one-step HI method (solid line), and influence of immersion time in the BSA solution of the two-step HI on BSA infiltration following immersion for 3 min in a 5.32% NaCl solution (broken line). The standard error is indicated by the vertical bracket at each observation point.

The uptake of BSA from the HI solutions at various pH's was evaluated by adjusting the one-step HI solution with 1 N HCl or 1 N NaOH to pH 5, 7, or 9. Similarily the two-step HI solutions were used together at pH 5, 7, or 9, but in addition, the opposite pH extremes were tested by using a pH 5 hyperosmotic priming solution followed by a pH 9 BSA solution and vice versa. Fish were immersed and sampled as previously described.

Results

The osmotic pressure of the one-step HI solution had to be above 1200 mosM to significantly increase plasma BSA above levels obtained from BSA–water solutions alone, and an immersion time of 30 s resulted in uptake of BSA from the BSA solution of the two-step HI (Fig. 1). Longer exposure in this solution caused no further increase in plasma BSA, except perhaps the 12-min immersion. However, this difference was not statistically significant and was not considered of enough practical value to warrant additional investigation.

The plasma-BSA levels that resulted from immersion in the one-step HI at various pH values showed a significant ($P = 0.01$) increase from 109 μg/mL at pH 5 to 209 μg/mL at pH 9 (Fig. 2). However, this trend was not observed when the same pH values were used in both solutions of the two-step HI. Uptake of BSA was best in this test when both the two-step HI solutions were used at pH 7 (100 μg BSA/mL plasma). We conducted further tests using the solutions of the two-step HI method adjusted to opposite pH extremes. When the

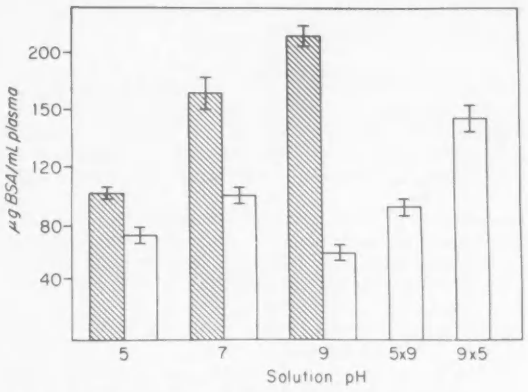

FIG. 2. Influence of solution pH on BSA infiltration into rainbow trout plasma from the one-step HI (shaded) or from the two-step HI (unshaded). The two bars at the right illustrate different pH's of solutions in the two-step HI; below the baseline, the pH of the NaCl solution is given first and that of the BSA solution second. The standard error is indicated by the vertical bracket at each observation point.

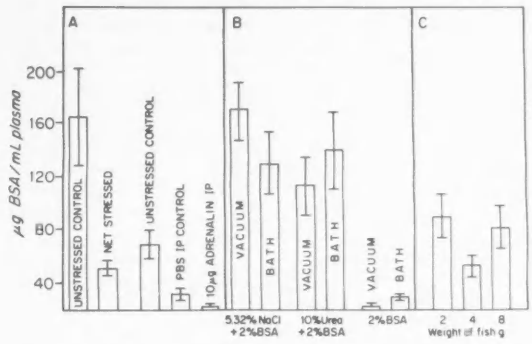

FIG. 3. A, Influence of stress on BSA infiltrations. Fish were stressed by holding them out of water in a net for 2 min or by injecting them with epinephrine (adrenaline) before their immersion in the one-step HI. B, Influence of vacuum on BSA infiltration. Fish were subjected to a reduced atmospheric pressure (250 mm Hg) while immersed in isosmotic concentration of urea or NaCl (one-step HI). Controls were immersed in identical solutions without the use of vacuum. C, Influence of fish weight on BSA infiltration from the one-step HI.

hyperosmotic NaCl solution was used at pH 5 followed by a pH 9 BSA solution, fish took up significantly less ($P = 0.01$) BSA than when the hyperosmotic solution was pH 9, followed by a BSA solution of pH 5 (Fig. 2).

Stress adversely affected BSA uptake by fish exposed to the one-step HI (Fig. 3A). Regardless of the source of the stress, plasma BSA levels were reduced. Net-stressed fish took up significantly less BSA compared with unstressed controls ($P = 0.01$). Fish stressed by injection of PBS or epinephrine also took up significantly less ($P = 0.05$) BSA than the noninjected control fish.

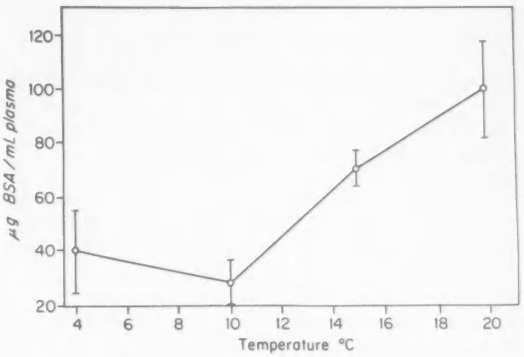

FIG. 4. Influence of temperature on BSA infiltration. Fish were acclimated and immersed in the one-step HI at 4–20°C. The standard error is indicated by the vertical bracket at each observation point.

Vacuum and fish size had no apparent effect on the infiltration of BSA into fish (Fig. 3B, C). The amount of BSA uptake was influenced only by the osmotic pressure, whether by NaCl or urea.

In fish acclimated and subjected to one-step HI at 4–20°C to determine the influence of temperature on BSA uptake, the amount of BSA infiltrated into the plasma increased significantly ($P = 0.05$), from 10 to 20°C (Fig. 4). There was no difference in BSA uptake at 4°C when compared with the uptake at 10°C.

Discussion

The data show that osmotic pressure, pH, and water temperature directly affect the amount of BSA taken into the plasma of rainbow trout and that the uptake of BSA from the two-step HI procedure is rapid. Care should be taken when fish are handled because stress reduced the uptake of BSA. In fact, the variable levels of BSA in control fish between tests indicate that the fish may not have been under the same stress conditions between tests. Fish weight (in the range of 2–8 g) apparently is not an important variable.

Amend and Fender (1976) presented the BSA model for vaccinating fish. Croy and Amend (1977) showed that HI of vibrio bacterin is an effective method of immunizing fish against vibriosis. Also HI could probably be used for administering pharmaceuticals as well as vaccines and other biologics. However, the conditions that optimize the infusion of BSA into rainbow trout may not apply to other substances or species and could vary with molecular size, conformation, and charge. Different conditions will likely have to be identified to optimize the infiltration of other materials.

In preliminary tests when vacuum was used in combination with hyperosmotic solutions, it was believed that vacuum caused infiltration of vaccine (Amend

1976). In fact field tests for control of vibriosis were conducted in which vacuum and hyperosmotic solutions were used, and these were highly effective (Antipa and Amend 1977). However, the data presented here and those reported by Croy and Amend (1977) indicate that the use of vacuum is equivocal and that the success of the previous tests can best be explained by other factors.

Amend and Fender (1976) proposed that the lymphatic system associated with the lateral line was the route of BSA entry into the circulatory system, but that the gills might also be involved. The epinephrine and net-stress test results presented here appear to exclude the gills as a major route of entry. Epinephrine or physical stress cause fish to increase the effective functional area of the gills (Bergman et al. 1974), and this increase should increase gill uptake of BSA from bath solutions. However, uptake of BSA was greatly reduced. This corroborates the earlier indication that the gills are probably not the major route of BSA entry, but additional studies are needed to show conclusively that the lateral line is the primary route. Further experimental use of this procedure with various vaccines is necessary to show the relation between the lateral line or gill and protective immunity.

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Survival of the Salmonid Viruses Infectious Hematopoietic Necrosis (IHNV) and Infectious Pancreatic Necrosis (IPNV) in Ozonated, Chlorinated, and Untreated Waters

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WEDEMEYER, G. A., N. C. NELSON, AND C. A. SMITH. 1978. Survival of the salmonid viruses infectious hematopoietic necrosis (IHNV) and infectious pancreatic necrosis (IPNV) in ozonated, chlorinated, and untreated waters. J. Fish. Res. Board Can. 35: 875–879.

Ozone and chlorine inactivation curves were determined in three water types at 10°C for the fish pathogenic viruses infectious hematopoietic necrosis (IHNV) and infectious pancreatic necrosis (IPNV). In phosphate-buffered, distilled water (PBDW) an ozone dose of 0.01 mg/L for 30 or 60 s inactivated IHNV or IPNV, respectively, suspended at a tissue culture 50% infective dose (TCID50) of 10^4–10^5/mL. In hard (120 mg/L as $CaCO_3$) and soft water (30 mg/L) lake waters, an ozone application rate of 70 mg·h^{-1}·L^{-1} for 10 min destroyed IHNV. IPNV inactivation in hard water required 90 mg O_3·h^{-1}·L^{-1} for 10 min but only a 30-s contact time in soft water. The IPNV was also somewhat more resistant to chlorine. In PBDW, a residual of 0.1 mg/L with contact times of 30 and 60 s, respectively, destroyed IHNV and IPNV. In soft lake water IHNV was destroyed within 5 min at 0.5 mg/L, while in hard water a 10-min contact time was required. For IPNV disinfection in soft water, 0.2 mg/L for 10 min was sufficient but this chlorine residual had essentially no effect on IPNV in hard water. Increasing this dose to 0.7 mg/L destroyed IPNV in hard water within 2 min. In untreated waters, IPNV was stable for at least 8 wk in either distilled, soft, or hard lake waters. However, IHNV survived only about 2 wk in distilled and 7 wk in the soft or hard lake waters. We suggest the serious consideration of ozone as a fish disease control agent.

Key words: ozone, chlorine disinfection, fish pathogens, viruses

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Nous avons établi les courbes d'inactivation de l'ozone et du chlore dans trois types d'eau à 10°C à l'endroit des virus pathogènes des poissons, celui de la nécrose hématopoïétique infectieuse (IHNV) et celui de la nécrose pancréatique infectieuse (IPNV). Dans de l'eau distillée tamponnée de phosphate (PBDW), une dose d'ozone de 0.01 mg/L pendant 30 à 60 s rend inactif l'IHNV ou l'IPNV respectivement, en suspension de dose de culture tissulaire infectieuse à 50% (TCID50) de 10^4 à 10^5/mL. Dans de l'eau de lac dure (~20 mg/L comme $CaCO_3$) et douce (30 mg/L), un taux d'application d'ozone de 70 mg·h^{-1}·L^{-1} durant 10 min détruit l'IHNV. L'inactivation de l'IPNV en eau dure nécessite 90 mg O_3·h^{-1}·L^{-1} durant 10 min, mais un contact de seulement 30 s en eau douce. L'IPNV est également un peu résistant au chlore. Dans de la PBDW, un résidu de 0.1 mg/L avec durée de contact de 30 s et de 60 s, respectivement, détruit l'IHNV et l'IPNV. Dans de l'eau de lac douce, l'IHNV est détruit en dedans de 5 min à 0.5 mg/L, alors que dans de l'eau dure, un contact de 10 min est nécessaire. Pour la désinfection de l'IPNV dans de l'eau douce, il suffit d'un contact de 10 min à 0.2 mg/L, mais ce résidu de chlore n'a pratiquement pas d'effet sur l'IPNV en eau dure. Si l'on augmente cette dose à 0.7 mg/L, l'IPNV en eau dure est détruit en dedans de 2 min. Dans des eaux non traitées, l'IPNV est stable pendant au moins 8 sem, soit dans de l'eau distillée, soit dans de l'eau de lac douce ou dure. Cependant, l'IHNV ne survit que 2 sem environ dans de l'eau distillée et 7 sem dans de l'eau de lac douce ou dure. On devrait considérer sérieusement l'ozone comme agent de contrôle des maladies des poissons.

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NONPERSISTENT disease control agents are needed in several phases of intensive fish culture such as destroying bacterial and viral fish pathogens in hatchery influent and effluent water (Conrad et al. 1975; Wedemeyer and Nelson 1977). Ozone has been shown to be effective against bacterial fish pathogens at concentrations as low as 0.01 mg/L, depending on water chemistry and contact time (Wedemeyer and Nelson 1977). Ozone is known to be effective against human viral pathogens (Majumdar and Sproul 1974; Burleson et al. 1975) but there is no information available on the conditions needed to destroy fish viral pathogens.

The objective of the present study was to determine ozone dose and contact times needed to destroy two common salmonid pathogenic viruses: infectious hematopoietic necrosis (IHNV) and infectious pancreatic necrosis (IPNV) under controlled laboratory conditions in ozone demand-free, phosphate-buffered, distilled water and in soft and hard waters representative of hatchery practice. Chlorine inactivation curves and virus survival times in untreated water were also determined for comparative purposes, and because of their practical importance.

Materials and Methods

IHNV, Wenatchee River strain (Amend and Wood 1972), was grown at 15°C on FHM (fathead minnow, *Pimephales promelas*) monolayer tissue cell cultures. IPNV, Powder Mill strain (Lientz and Springer 1973), was grown on RTG-2 (rainbow trout, *Salmo gairdneri*, gonad) cells at 15°C. All cell cultures were maintained in Eagle's minimal essential medium containing 10% agamma fetal calf serum (MEM-10). Earle's balanced salt solution was used with penicillin and streptomycin added at 100 IU/mL and 100 μg/mL, respectively.

When the viral cytopathic effects on the cells were maximal, the tissue culture fluid was centrifuged at 2000 $\times$ *g* for 10 min and the supernatant containing the IHNV was collected and held frozen at −70°C until needed. The IPNV supernatant was held at 10°C until needed. Two hours before use, a portion of the virus suspension was centrifuged for 1 h at 54 000 $\times$ *g* and the resulting viral pellet resuspended in demineralized water. This suspension was sonicated for 30 s to break up virus aggregates.

Batch disinfection tests of both ozone and chlorine were carried out in autoclaved water at 10°C in an insulated contact chamber modified from Majumdar et al. (1973).

TABLE 1. Water chemistry summary of the autoclaved distilled water (DW) and soft (SLW) and hard (HLW) lake waters used in the disinfection tests. (JTU — Jackson Turbidity Units.)

Parameter	Water type		
	DW	SLW	HLW
Total hardness (mg/L $CaCO_3$)	0	30	120
Total dissolved solids (mg/L)	0	42	440
Acidity (pH)	6.9	6.9	8.2
Turbidity (JTU)	0	3	7

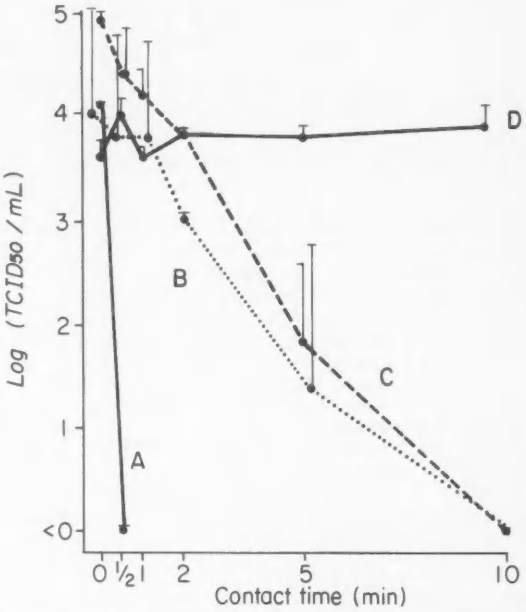

FIG. 1. IHNV inactivation by ozone. A, 0.01 mg O_3/L in ozone demand-free, phosphate-buffered, distilled water; B and C, 70 mg $O_3 \cdot h^{-1} \cdot L^{-1}$ in hard and soft lake water; D, control, 10°C. Because stable ozone residuals were unobtainable in the two natural waters, application rates are given. Virus counts are shown as $\bar{x} + SE$ (lines for $\bar{x} - SE$ were deleted to improve readability of the figure).

Air flow through the mixing sparger, other contact chamber operating parameters, and the sampling regimen were as previously described (Wedemeyer and Nelson 1977).

Ozone was generated by a Pollution Control Industries model C2P-3C ozonator; residuals in distilled water were measured by the method of Schecter (1973). This procedure was not satisfactory for measuring low levels of ozone in the lake waters, so the *N*, *N*-diethyl-*p*-phenylenediamine (DPD) chlorine method, with the factor 0.60 to convert to ozone, was used (APHA et al. 1971).

For the chlorine tests, sufficient sodium hyphochlorite to slightly exceed the chlorine demand was added ("breakpoint chlorination"). The resulting residuals were measured by the standard DPD chlorine procedure.

The water types tested were ozone and chlorine demand-free, double distilled (0.007 M in phosphate buffer, pH 7); soft lake water (20 mg/L hardness as $CaCO_3$); and hard lake water (120 mg/L). Table 1 summarizes the water chemistry description.

For the virus assay, 1-mL water samples were taken from the contact chamber, added to 1 mL of double strength MEM-10, 0.05 M in sodium thiosulfate to neutralize any remaining chlorine or ozone, placed on FHM or RTG-2 tissue culture cells, and incubated at 12 or 18°C, respectively. The controls were (1) cells only, (2) cells with thiosulfate-neutralized chlorinated or ozonated virus-free water added. The microtiter plate technique described by Gratzek et al. (1973) was used. The tissue culture 50% infective dose (TCID50) was calculated using the method of Reed

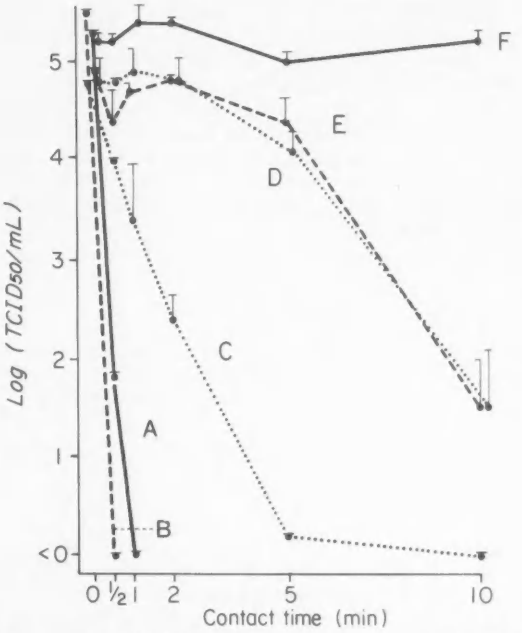

FIG. 2. IPNV inactivation by ozone. A, 0.01 mg O_3/L in ozone demand-free, phosphate-buffered, distilled water; B and C, 90 mg $O_3 \cdot h^{-1} \cdot L^{-1}$ in soft and hard lake water; E and D, 70 mg $O_3 \cdot h^{-1} \cdot L^{-1}$ in soft and hard lake water; F, control, 10°C. Because stable ozone residuals were unobtainable in the two natural waters, application rates are given. Virus counts are shown as $\bar{x} + SE$.

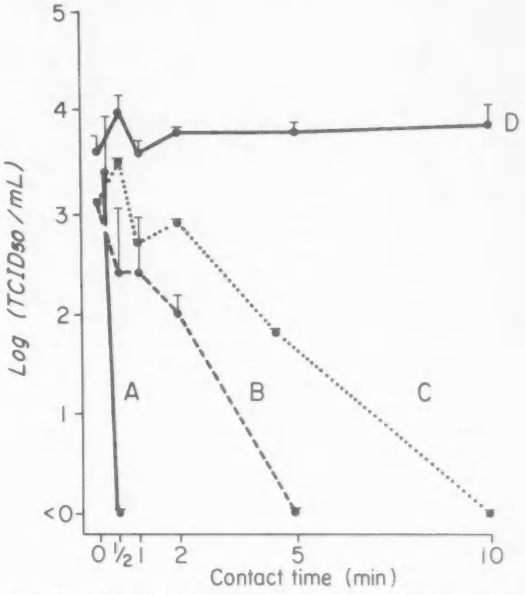

FIG. 3. IHNV inactivation by chlorine. A, 0.1 mg/L in chlorine demand-free, phosphate-buffered, distilled water; B and C, 0.5 mg/L in soft and hard lake water; D, control, 10°C. Stable residuals were obtained in all water types. Virus counts are given as $\bar{x} + SE$.

and Muench (1938). All tests were run in duplicate.

Survival curves for IPNV and IHNV in untreated waters were determined by suspending virus particles at about 10^5 TCID50/mL in 100-mL autoclaved samples of the distilled, soft, or hard lake water incubated at 10°C. Virus titers were determined weekly for 2 mo using standard microtiter plate techniques.

Results and Discussion

Ozone applied at a rate of 70 mg $\cdot h^{-1} \cdot L^{-1}$ to ozone demand-free, phosphate-buffered, distilled water in the contact chamber came to equilibrium at a residual of 0.01 mg/L. This was sufficient to inactivate 10^4–10^5 TCID50/mL IHNV within 30 s (Fig. 1). In the two natural waters, a stable ozone residual was difficult to achieve. However, the same 70 mg $\cdot h^{-1} \cdot L^{-1}$ generation rate, with 10 min contact time was sufficient to inactivate IHNV in both hard and soft lake waters (Fig. 1). In contrast, complete IPNV disinfection in hard lake water required 90 mg $O_3 \cdot h^{-1} \cdot L^{-1}$ with a 10-min contact time (Fig. 2). In soft lake water, the IPNV was inactivated in about 30 s at this O_3 dosage. However, 60 s of contact time at 0.01 mg/L was needed for a complete kill in ozone demand-free, phosphate-buffered, distilled water (Fig. 2). Thus, of the two viruses, IHNV seems to be somewhat more intrinsically sensitive to ozone.

A stable chlorine residual, in contrast to ozone, was easily achieved in all three water types by adding sufficient NaOCl to slightly exceed the chlorine demand ("break-point chlorination"). IHNV was inactivated within 30 s and IPNV within 1 min at 0.1 mg/L in the chlorine demand-free, phosphate-buffered, distilled water (Fig. 3, 4). Thus, IHNV also appears to be more intrinsically sensitive to chlorine. However, in the two natural waters, it was necessary to increase the chlorine dose substantially to achieve rapid inactivation of these viruses. For IHNV disinfection in hard lake water, 0.5 mg/L for 10 min was sufficient (Fig. 3), while increasing the chlorine dose to 1 mg/L reduced the required contact time to 30 s (not shown). Soft lake water was easier to disinfect (Fig. 3); the 0.5 mg/L chlorine level required only a 5-min contact time.

For IPNV disinfection, the soft lake water again offered the least protection. A chlorine level of 0.2 mg/L inactivated the virus within 10 min, whereas in hard water this concentration had essentially no effect (Fig. 4). However, increasing the chlorine dose to 0.7 mg/L destroyed IPNV within 2 min (Fig. 4).

Virions of IHNV possess lipoprotein envelopes which are lacking in the IPNV. These lipoproteins would be expected to be readily susceptible to oxidative damage by chlorine and thus infectivity would be easily de-

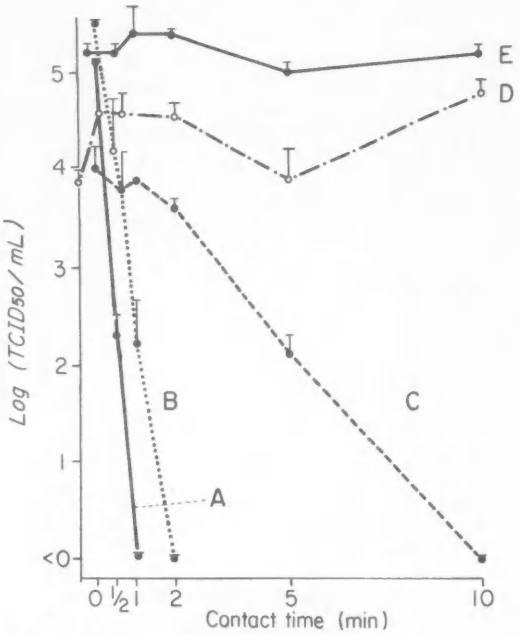

FIG. 4. IPNV inactivation by chlorine. A, 0.1 mg/L in chlorine demand-free, phosphate-buffered distilled water; B, 0.7 mg/L in hard water; C and D, 0.2 mg/L in soft and hard water; E, control, 10°C. Stable residuals were obtained in all water types. Virus counts are given as $\bar{x} + SE$.

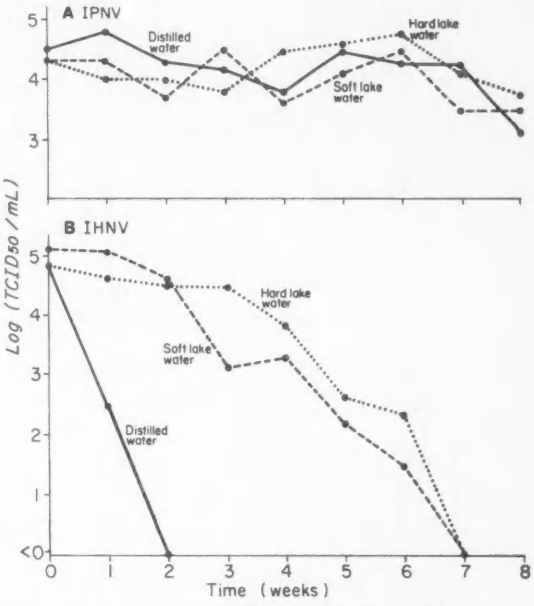

FIG. 5. Survival of (A) IPNV and (B) IHNV in untreated distilled and soft and hard lake waters, 10°C.

stroyed. However, because ozone has a substantially higher redox potential, the role of envelope susceptibility in disinfection would be expected to be less important because of the overwhelming oxidative attack.

Previous workers have noted similar patterns of susceptibility for IHNV and IPNV. Desautels and MacKelvie (1975) reported that chlorine (gas) added at 25 mg/L with a 30-min contact time inactivated IPNV. Amend and Pietsch (1972) showed that sodium hypochlorite added at 10 mg/L for 30 min inactivated IHNV. The much lower chlorine requirement demonstrated by the present work may be due to the following: chlorine was added until a stable residual developed (i.e. "break-point chlorination"); intermediate contact times were sampled; chlorine residuals were measured rather than calculated from the amount added; and, possibly, different virus strains were used.

For completeness, and because of its importance in fish disease control, the survival times of the two viruses in untreated water were also determined (Fig. 5). IPNV was the most stable and suffered essentially no loss in titer during 8 wk of incubation in distilled water or in soft, or hard lake water (Fig. 5A). IHNV was both less stable and more affected by water chemistry (Fig. 5B). The titer decreased to 1 TCID50/mL (minimum detection limit) within 2 wk in distilled water. The titer in the soft and hard lake waters was retained longer, but decreased to 0 in about 7 wk (Fig. 5B).

Previous workers have reported a range for IPNV stability in untreated fresh water from just 10 days at 4°C (Tu et al. 1975) to more than 8 wk with a 2 log (99%) reduction in initial titer (Desautels and MacKelvie 1975). However, water chemistry information such as total hardness, total dissolved solids, and pH were not given. The present results in distilled, as compared with soft and hard lake waters, give evidence that IPNV stability does depend somewhat on water chemistry.

Less information has been published on IHNV survival in untreated waters. McAllister et al. (1974) reported a 1 log (90%) loss of infectivity for IHNV after 5 d in dechlorinated "tap water" and in distilled water, pH 6–8, 12°C. Pietsch et al. (1977) reported IHNV 99.9% inactivation times of about 10 d in distilled water, over the pH range 6–8. Survival was 4 times longer than in seawater. Mineral additions to increase distilled water total hardness to up to 300 mg/L (as $CaCO_3$) had no significant effect on survival. However, the present results indicate that much longer survival times are possible in either hard or soft lake water and that IHNV stability must be enhanced by water chemistry factors other than mineralization.

In summary, the IHNV is somewhat more sensitive to ozone disinfection than is IPNV. However, in ozone demand-free water only 0.01 mg/L O_3 with a contact time of 30–60 s was required to inactivate either virus.

Their intrinsic resistance to chlorine also differed somewhat. A 0.1-mg/L dose with a 2-min contact time was required for IPNV inactivation in chlorine demand-free water compared with only a 30-s contact time for IHNV. Survival of both viruses in untreated hard or soft lake water was so prolonged that sufficient natural die-off for disease control is unlikely unless the reservoir of infection, such as a salmon spawning ground, is quite distant from the hatchery intake. Based on the present results, ozone should be seriously considered a fish disease control agent.

Acknowledgments

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Relationship Between Cytoplasmic Distribution of Mercury and Toxic Effects to Zooplankton and Chum Salmon (*Oncorhynchus keta*) Exposed to Mercury in a Controlled Ecosystem

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BROWN, D. A., AND T. R. PARSONS. 1978. Relationship between cytoplasmic distribution of mercury and toxic effects to zooplankton and chum salmon (*Oncorhynchus keta*) exposed to mercury in a controlled ecosystem. J. Fish. Res. Board Can. 35: 880–884.

Fish and zooplankton were simultaneously exposed to trace, 1, and 5 μg Hg/L. In fish and zooplankton, pathological effects appeared to coincide with saturation of metallothionein and "spillover" of Hg into the high molecular weight protein (enzyme-containing) pool. Coincidental with increases of Hg in tissue were decreases of Cu and Zn. Pathological effects of Hg are explained in terms of tertiary and quaternary structural changes in metalloenzymes resulting from replacement of Cu and Zn by Hg. Decreases in tissue Cu and Zn with increasing Hg concentration are discussed as an intracellular displacement of Cu and Zn by Hg and as duodenal and cellular exclusion processes.

Key words: CEPEX, *Oncorhynchus keta*, zooplankton, mercury, copper, zinc, metallothionein, enzymes, metal tolerance

BROWN, D. A., AND T. R. PARSONS. 1978. Relationship between cytoplasmic distribution of mercury and toxic effects to zooplankton and chum salmon (*Oncorhynchus keta*) exposed to mercury in a controlled ecosystem. J. Fish. Res. Board Can. 35: 880–884.

Nous avons exposé simultanément des poissons et du zooplancton à du mercure en traces, et à des teneurs de 1 et 5 μg Hg/L. Chez les poissons, tout comme dans le zooplancton, les effets pathologiques semblent coincïder avec la saturation de métallothionéine et le « déversement » de Hg dans la masse (contenant des enzymes) de protéines de poids moléculaires élevés. En même temps que le Hg augmente dans le tissu, le Cu et Zn diminuent. Nous expliquons les effets pathologiques de Hg en fonction de changements structuraux tertiaires et quaternaires dans les métalloenzymes résultant du remplacement de Cu et de Zn par Hg. Nous analysons la diminution de Cu et de Zn dans le tissu avec l'augmentation de la teneur en Hg comme étant à la fois un déplacement intracellulaire de Cu et de Zn par Hg et comme processus d'exclusion duodénale et cellulaire.

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HEAVY metals such as Hg, Cd, Cu, and Zn are toxic to organisms but prior exposure to these metals can result in acquired tolerance to increasing metal levels (Bryan and Hummerstone 1971; Bremner 1974). Tolerance occurs as a result of synthesis of the protein metallothionein (Leber 1974; Piscator 1964). Metallothionein is a low molecular weight (10 000) protein high in sulfhydryl groups due to the presence of high levels of the amino acid cysteine (Margoshes and Vallee 1957; Kagi and Vallee 1960). The sulfhydryl groups can bind or chelate Hg, Cd, Ag, Cu, Sn, and Zn (Winge et al. 1975; Sabbioni and Marafante 1975) thus rendering them less toxic to the exposed organism (Piscator 1964). Metallothionein is usually stored solubilized in liver and kidney cytoplasm in higher organisms.

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One obvious means by which metallothionein-mediated tolerance to heavy metals might be acquired would be by synthesis of excesses of this protein upon initial exposure. This excess metallothionein would then be readily available to quickly bind and detoxify heavy metals upon subsequent exposure. However, it is known that metallothionein always exists in the saturated state in organisms, i.e. one metal ion for each three cysteine residues (Kagi and Vallee 1960, 1961; Pulido et al. 1966; Buhler and Kagi 1974; Bremner and Davies 1975). Recently it has become apparent that metallothionein produced in response to Cd, Hg, Ag, or Cu contains Zn in approximately half of its binding sites (Leber 1974; Bremner and Davies 1975; Winge et al. 1975). This Zn has a much lower affinity than Cd or Hg for metallothionein binding sites (Kagi and Vallee 1960; Pulido et al. 1966). Upon a second exposure to Cd or Hg, these elements replace Zn on metallothionein

so that Zn is released into the cytoplasm rather than Cd or Hg (Leber 1974). Zinc is relatively nontoxic compared with Cd or Hg (Bremner 1974).

If an organism is exposed to a very high dose of Cd or Hg, then there may not be enough Zn-containing binding sites on metallothionein to detoxify all of the Hg or Cd. Further, de novo synthesis of metallothionein may be slower than the rate of influx of these metals. These conditions will result in a "spillover" of Hg or Cd to the enzyme pool. This "spillover" coincides with the appearance of pathological effects (Winge et al. 1973; Brown 1977; Brown et al. 1977; Irons and Smith 1976).

Mercury and cadmium exert their toxic effects by replacing Cu and Zn in metalloenzymes. This changes the three dimensional conformation of these enzymes so substrate molecules no longer fit binding sites (Friedberg 1974), or splits enzymes into subunits (Gerhart and Schachman 1965; Jovin et al. 1969) so that regulation of enzyme activity may be lost (White et al. 1968; Brown et al. 1977; Brown 1977).

When Cd or Hg displaces Cu or Zn from metallothionein, these latter metals may also appear in the high molecular weight protein (enzyme-containing) pool. However, as Cu and Zn are natural components of many metalloenzymes (Friedberg 1974), they are relatively nontoxic compared with Cd or Hg (Bremner 1974).

This study reports findings on the relationship of previously reported growth reduction of fish and zooplankton exposed to Hg (Koeller and Wallace 1977) with "spillover" of Hg from metallothionein to the enzyme pool.

Materials and Methods

The CEPEX (Controlled Ecosystem Pollution Experiment) facility consists of 1350-m^3 polyethylene controlled experimental ecosystems (CEEs) suspended in Saanich Inlet, Victoria (Menzel and Case 1977). These simulate the natural water column, except for the effects of large lateral currents and sediment recycling. An experiment was conducted in the summer of 1976 to determine the impact of Hg on the marine ecosystem. On day 1 of this experiment a portion of the natural pelagic population of Saanich Inlet was captured into each of three CEEs. Chum fry were added on day 10. Also on day 10, mercury (in the form of $HgCl_2$) was introduced into two of the CEEs to produce final concentrations of 5 and 1 μg/L. Uniform distribution of mercury was aided by use of a diffuser ring lowered to 10 m below the surface (Topping and Windom 1977). Mercury concentrations decreased throughout the experiment at a rate of approximately 2%/d. This decrease occurred due to attachment of Hg to settling particulate matter greater than 10 000 mol wt. By day 72, Hg levels were approximately one tenth those of initial concentrations (Grice et al. 1977).

On day 72, zooplankton were sampled using a 25-μm mesh net as described by Grice et al. (1977). The zooplankton were drained of excess water and frozen at −20°C. Fish were captured with a specially designed seine and similarly frozen until analyzed. Three fish from each exposure were randomly selected for analysis in the present study.

Fish livers or zooplankton were later thawed, homogenized in 0.9% NaCl, and centrifuged at 27 000 × g. The supernatant was collected, the pellet rehomogenized in 0.9% NaCl and centrifuged at 27 000 × g. Supernatants were combined, heated to 70°C for 1 min (Webb 1972), and centrifuged at 27 000 × g. The supernatant of this final centrifugation was applied to a 100 × 1.6 cm Pharmacia column containing Pharmacia G-75 gel. Fractions were collected and measured at 250 and 280 nm on a Perkin Elmer spectrophotometer. The Cu and Zn contents of the fractions were measured on a Perkin Elmer 303 atomic absorption spectrophotometer using the flame method with deuterium arc background correction. Mercury was measured by a cold vapor method utilizing a 30-cm cell (Pharmacia UV Control Unit model 100, Pharmacia UV Optical Unit model 100). Analytical precision for Cu was $\bar{x} \pm 3.3\%$ (mean ± SD, $N = 15$), for Zn $x \pm 3.5\%$ (mean ± SD, $N = 15$), and for Hg $x \pm 6.0\%$ (mean ± SD, $N = 15$).

By comparing protein absorbance and metal profiles with those found in previous studies (Casterline and Yip 1975; Leber 1974; Olafson and Thompson 1974; Marafante 1976; Brown et al. 1977; Brown 1977), fractions were identified as belonging to the high molecular weight protein (enzyme-containing) pool, metallothionein, or the low molecular weight cytoplasmic pool. The Cu and Zn levels in fractions comprising these cytoplasmic pools were added together, to give the total level of each metal in each pool. Mercury was determined on one composite sample of each pool as it was not detectable in individual fractions. Metal levels in each pool were then calculated per gram of tissue extracted.

Results

The most prominent change is the very large increase of Hg in the high molecular weight protein (enzyme-containing) pool of fish and zooplankton exposed to 5 μg Hg/L (Tables 1 and 2). There appears to be a limit to Hg-thionein production reached at the 1-μg Hg/L exposure, as there is little increase in Hg-thionein from 1 to 5 μg Hg/L. When this limit of Hg-thionein production is apparently reached, excesses of Hg appear in the high molecular weight protein pool.

In fish liver cytoplasm, there are decreases of total Cu and Zn with increasing Hg exposure. These decreases appear to be a reflection of decreases of both Cu and Zn in the enzyme-containing pool, of Cu in metallothionein, and of Zn in the low molecular weight cytoplasmic pool (Table 1).

In cytoplasm of zooplankton exposed to 5 μg Hg/L, Cu appears to decrease in the enzyme-containing pool, increase in metallothionein, and decrease in the low molecular weight cytoplasmic pool, resulting in a net decrease in cytoplasmic Cu (Table 2). Copper levels are relatively unchanged by exposure to 1 μg Hg/L. At both mercury exposures, Zn in zooplankton cytoplasm appears to be unchanged in the enzyme-containing pool, while it increased in metallothionein, and decreased in the low molecular weight cytoplasmic pool. Thus, there is a net decrease in cytoplasmic Zn (Table 2).

TABLE 1. Distribution of Hg, Cu, and Zn among cytoplasmic pools from liver of chum salmon exposed to various concentrations of Hg. MW, molecular weight; ND, not detectable.

Hg exposure concn (μg Hg/L)	Metal	Cytoplasmic total (μmol metal/g tissue, wet wt)	High MW protein pool (μmol metal/g tissue, wet wt)	Metallothionein (μmol metal/g tissue, wet wt)	Low MW cytoplasmic pool (μmol metal/g tissue, wet wt)
Control	Hg	0.61×10^{-3}	0.11×10^{-3}	0.29×10^{-3}	0.22×10^{-3}
	Cu	1.832	0.592	0.532	0.708
	Zn	0.164	0.111	ND	0.053
1	Hg	0.87×10^{-3}	0.23×10^{-3}	0.35×10^{-3}	0.29×10^{-3}
	Cu	1.558	0.402	0.424	0.733
	Zn	0.104	0.071	ND	0.033
5	Hg	4.77×10^{-3}	4.04×10^{-3}	0.38×10^{-3}	0.35×10^{-3}
	Cu	1.445	0.353	0.347	0.745
	Zn	0.114	0.075	ND	0.039

TABLE 2. Distribution of Hg, Cu, and Zn among cytoplasmic pools from tissue of zooplankton exposed to various concentrations of Hg. MW, molecular weight; ND, not detectable.

Hg exposure concn (μg Hg/L)	Metal	Cytoplasmic total (μmol metal/g tissue, wet wt)	High MW protein pool (μmol metal/g tissue, wet wt)	Metallothionein (μmol metal/g tissue, wet wt)	Low MW cytoplasmic pool (μmol metal/g tissue, wet wt)
Control	Hg	0.40×10^{-4}	0.32×10^{-4}	0.04×10^{-4}	0.04×10^{-4}
	Cu	0.359	0.041	0.033	0.286
	Zn	0.299	0.012	ND	0.288
1	Hg	0.96×10^{-4}	0.40×10^{-4}	0.27×10^{-4}	0.28×10^{-4}
	Cu	0.352	0.046	0.039	0.267
	Zn	0.283	0.016	0.005	0.262
5	Hg	1.93×10^{-4}	1.17×10^{-4}	0.26×10^{-4}	0.50×10^{-4}
	Cu	0.326	0.031	0.045	0.249
	Zn	0.212	0.011	0.026	0.175

Discussion

Results of this study and those of Koeller and Wallace (1977) appear to support the "spillover" theory (Winge et al. 1973; Brown et al. 1977). This theory suggests that intracellular toxic effects of Cd and Hg will not occur unless and until these metals appear in the enzyme-containing pool. These metals will spillover from metallothionein to the enzyme-containing pool when the binding capacity of metallothionein is exceeded. In the present study, it appears that the binding capacity of metallothionein was surpassed in the 5-μg Hg/L exposure. Mercury-thionein increased from the control to the 1-μg Hg/L exposure, but increased very little from 1 to 5 μg Hg/L. Rather, at 5 μg Hg/L, excess Hg occurred in the enzyme-containing pool.

Koeller and Wallace (1977) found fish and zooplankton growth to be decreased in these same 5-μg Hg/L CEEs. On day 72, fish exposed to 5 μg Hg/L weighed about 6 g while controls or 1-μg Hg/L exposed fish weighed 12.5 g. Zooplankton counts in the 5-μg Hg/L CEEs were one fourth those of control or 1-μg Hg/L exposed zooplankton counts on day 72. Thus, at that concentration of Hg exposure where there was a dramatic increase of Hg in the enzyme-containing pool, there was a similar dramatic decrease in growth. At least in part, therefore, reduced growth may be a result of inhibition or alteration of enzyme functioning by Hg (Friedberg 1974; Bremner 1974; Brown et al. 1977; Brown 1977).

Most likely, toxic effects result from a change in metalloenzyme tertiary or quaternary structure when Cu or Zn is displaced by Hg in these enzymes (Friedberg 1974; Bremner 1974). In the present study, with increases of Hg in the enzyme-containing pool, there were decreases of Cu and Zn. Since Hg exposure results in a reduction of Cu and Zn in the enzyme-containing pool, Hg exposure might result in metal deficiency effects. Thus, growth decreases could occur independent of the other enzymatic inhibitory toxic effects of Hg, due simply to decreases of Cu and Zn (Underwood 1971).

While intracellular displacement of Cu and Zn by Hg partially explains cellular losses of these metals, exclusion of uptake of these metals is also a possibility. As explained by Sugawara and Sugawara (1975) and Stonard and Webb (1976), gastrointestinal uptake of Hg, Cd, Cu, and Zn occurs via duodenal mucosal metallothionein. When exposed to high levels of Cd or Hg, this metallothionein is saturated by Cd or Hg. It then cannot bind Cu and Zn, and therefore they are

not absorbed into the bloodstream from the intestine (Stonard and Webb 1976).

Other workers (Fowler et al. 1975; Overnell 1975) found that Hg exposure results in a loss of certain cellular constituents including potassium. Overnell (1975) explains the losses as leakage due to membrane damage caused by Hg. DeFilippis and Pallaghy (1976) found that *Chlorella* exposed to Hg had decreased uptake of ^{65}Zn. They conclude that this decrease in uptake is due to an inhibition of the temperature sensitive component of Zn uptake and to a reduction in the number of exchange sites available for Zn in the cell wall. They attributed increased tolerance of *Chlorella* to trace elements as characterized by development of this exclusion mechanism.

In fish liver, as Hg increased in metallothionein, there was a concurrent decrease of Cu in metallothionein. This is consistent with Leber's (1974) theory suggesting that metallothionein results in detoxification, in part, by a displacement of less toxic metals from metallothionein by more toxic ones. Leber found that Cd displaced Zn from metallothionein. In the present study, Hg appears to have displaced Cu. Zinc in fish liver metallothionein was not detectable by methods employed here.

In zooplankton, both Cu and Zn increased in metallothionein with increases of Hg in metallothionein, even at the highest level where spillover occurred. Therefore, in zooplankton, Cu and Zn were not displaced by increasing levels of Hg in metallothionein, as occurred in fish. Discrepancies between fish and zooplankton may be due to different tissue types or to lesser Hg levels in zooplankton. Zooplankton cytoplasmic Hg levels at 5-μg Hg/L exposure were only one fifth those of fish liver cytoplasmic Hg levels at 1-μg Hg/L exposure and one twenty-fifth those of fish at 5-μg Hg/L exposure (Tables 1 and 2). In fish liver cytoplasm at 5-μg Hg/L exposure, 85% of Hg is found in the enzyme-containing pool, while in zooplankton cytoplasm only 60% of Hg is found in the enzyme-containing pool, indicating much less spillover in zooplankton. Therefore, the lesser levels of Hg in zooplankton would probably present less of a challenge to Cu and Zn in metallothionein.

It is evident from this and previous studies that toxic effects of Cd or Hg do not occur until "spillover" occurs. Whether or not spillover occurs will depend upon whether or not metallothionein synthesis can keep pace with metal inflow. Thus, exposure to low levels of Hg over a long period might result in very high tissue levels of Hg, but it is all bound to metallothionein and hence detoxified. Much shorter exposure periods with much higher levels of Hg exposure might result in lower tissue levels of Hg, but most of the Hg would appear in the enzyme-containing pool with concurrent toxic effects. Thus, the factor critical to an organism's survival may not be its tissue levels of Cd or Hg, but rather, whether these occur in the enzyme-containing pool or as metallothionein. This should depend upon the level and rate of exposure and uptake.

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Spatial Distribution of Nearshore Fish in the Vicinity of Two Thermal Generating Stations, Nanticoke and Douglas Point, on the Great Lakes

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MINNS, C. K., J. R. M. KELSO, AND W. HYATT. 1978. Spatial distribution of nearshore fish in the vicinity of two thermal generating stations, Nanticoke and Douglas Point, on the Great Lakes. J. Fish. Res. Board Can. 35: 885–892.

At Nanticoke, Lake Erie, 1974, mean fish density varied considerably, range 162–14 204/10 000 m^3, as estimated by digital acoustic fish enumeration. At Douglas Point, Lake Huron, 1975, mean density varied less, range 108–671/10 000 m^3. At both sites fish densities were generally greatest in the shallowest, 3–5 m, depths. At Nanticoke, where the nearshore has low relief, there were no distinguishable communities. At Douglas Point, where depth increases rapidly offshore, there was evidence of benthic and pelagic communities. There was no evidence of altered fish distribution in relation to temperature. At Nanticoke there was no vertical variation in temperature and no vertical response was to be expected. At Douglas Point there was thermal stratification present in the summer and there was no apparent response. The influence of incident radiation was uncertain because of the effects of diurnal migrations. At both locations fish were clustered horizontally to varying degrees in the spring and fall, while in the summer fish were distributed more evenly. Densest clusters were usually in the vicinity of the turbulent discharge at both locations. The lack of temperature response and the similarity of Nanticoke with situations at nearby streams on Lake Erie suggest that the fish are responding to currents and perhaps topography.

Key words: temperature, acoustic enumeration, topography, light

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A Nanticoke, Lac Erié, 1974, la densité moyenne des poissons, estimée par recensement acoustique numérique, varie grandement, allant de 162 à 14 204/10 000 m^3. A Douglas Point, Lac Huron, 1975, la densité moyenne varie moins, allant de 108 à 671/10 000 m^3. Aux deux endroits, les densités maximales se trouvent généralement dans les plus faibles profondeurs, 3 à 5 m. A Nanticoke, où le rivage est caractérisé par un bas relief, il n'y a pas de communautés distinctes. A Douglas Point, où la profondeur augmente rapidement à mesure qu'on s'éloigne du bord, on constate la présence de communautés benthiques et pélagiques. Nous n'avons pas constaté de changement dans la distribution des poissons en fonction de la tmpérature. A Nanticoke, il n'y a pas de variation verticale de température et on ne pouvait s'attendre à une différence dans la répartition verticale des poissons. A Douglas Point, il y a stratification thermique en été mais pas de réponse apparente. Nous n'avons pu déterminer avec certitude l'influence de la radiation incidente à cause des effets des migrations nycthémérales. Aux deux endroits, les poissons sont groupés horizontalement en agglomérations plus ou moins denses au printemps ou en automne, alors qu'en été ils sont répartis plus uniformément. Les groupes les plus denses se trouvent ordinairement dans le voisinage de l'effluent turbulent aux deux endroits. L'absence de réaction à la température et la ressemblance de Nanticoke avec des situations prévalant dans des cours d'eau du voisinage sur le lac Erié donnent à croire que les poissons réagissent aux courants et peut-être à la topographie.

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NUMEROUS factors, such as temperature, light, and current, influence the spatial distribution of fish in aquatic ecosystems. Until recently, opportunities to examine these factors acting in concert in nature have been limited. Kelso and Minns (1975) and others have shown that acoustic enumeration of fish expands our knowledge of the environmental interactions influencing fish distribution. These developments are timely in view of the concern generated over the impact of thermal discharges near the shores of lakes and oceans.

In this study we seek to extend our knowledge of fish distribution in the nearshore environment. In particular, we are concerned with the distribution of fish in the vicinity of two thermal generating stations on the Great Lakes: one, a nuclear plant on Lake Huron and the other, a coal-fired plant on Lake Erie.

Materials and Methods

THERMAL GENERATING PLANTS — NANTICOKE AND DOUGLAS POINT

The Nanticoke coal-fired generating station is located about 13 km east of Port Dover, Lake Erie. When the plant is completed sometime in 1977, the capacity will be 4000 megawatts (MW). At full load it will require 152 m^3/s of lake water. There are two intakes, a subsurface one and a channel cut in bedrock. During 1974, only a few of the eight generating units were operating intermittently; thus, outfall temperatures were only slightly above ambient water. The plant was not operating during September and October.

On acoustic census days, flow of cooling water ranged from 25.5 to 58.6 m^3/s. Temperature rise across the condensers (ΔT) averaged, on any day, between 0.4 and 3.9°C.

The lake in the vicinity of the station is generally shallow (5–8 m). There is rarely any vertical stratification of temperature in the area even during the summer (Nanticoke Environmental Committee 1973). Offshore, water currents generally follow the wind, while inshore, currents usually parallel the shoreline (Palmer and Walker 1973).

The Douglas Point nuclear generating station, Lake Huron, is located approximately halfway between Goderich and Southhampton. The station consists of one CANDU-type nuclear reactor with an output of 220 MW. Water is drawn from the lake via an offshore submerged tunnel. The water is shared by the Bruce Heavy Water Plant and Douglas Point Generating Station. The discharges of the two plants are combined and released onshore at the surface. The plant ran at essentially a constant level during 1975 and the flow of cooling water ranged from 21.6 to 24.8 m^3/s. Daily temperature rise across the condenser averaged 7.1–13.6°C.

Water depth increases rapidly offshore from Douglas Point (20 m at 1 km from shore). Currents generally follow the shoreline but are subject to frequent changes between north and south (Csanady 1970). Thermal stratification exists in summer with a thermocline evident in the range 10–25 m in August, depending on prevailing wind conditions. This area on the eastern shore of Lake Huron is subject to upwellings (Strong 1974).

DATA COLLECTION AND ANALYSIS

Fish density and distribution were assessed through the use of electroacoustic techniques designed for fish detection (Kelso et al. 1974; Kelso and Minns 1975; White 1976; Kelso 1977). Basically the system consisted of an 80 kHz EDO Western transceiver whose incoming signals were processed by a digital logic (Kelso et al. 1974; Kelso and Minns 1975) at Nanticoke and by an echo analysis control subsystem (White 1976; Kelso 1977) at Douglas Point. Data were stored by punched paper tape (Nanticoke) and mechanical digital printer (Douglas Point). Although echo-sizing capabilities existed, all data above the threshold (corresponds to a fish size of 6 cm on the acoustic axis) were grouped, since the reliability of the sizing process is still uncertain.

Census transects were conducted between marker buoys at both locations. At Nanticoke there were usually 8–10 transects run on each census day, while at Douglas Point there were 11–13 lines. During censuses, vessel speed remained constant.

At Nanticoke temperature was measured at three to five depths using a towed thermistor array (Kelso and Minns 1975) concurrent with the acoustic censuses. At Douglas Point a mechanical bathythermograph was used to measure temperature profiles at five to seven inshore and offshore stations immediately after a census. Incident radiation was continuously monitored hourly with a recording pyranometer at both locations during the operating periods.

Fish species composition was provided at Nanticoke by trap nets and gill nets (Teleki 1976) set near the discharge and at Douglas Point by our gill nets set near the discharge and at a "control" site. Two net sets of 12-h duration were made at each netting location.

Acoustic counts in each depth shell for each set of transmissions were converted to number per 10 000 m^3 (Kelso et al. 1974). When a depth shell overlapped the bottom, the volume swept was obtained by integrating along the echogram record of depth. Estimates were discarded when the actual volume swept was $<20\%$ of the volume that would be swept in open water.

After data condensation (Kelso and Minns 1975), counts for each census were sorted into a triangular matrix comprising the depth sorting shells (rows) and the corresponding bottom depth ranges (columns). An additional column was necessary when counts were obtained where the bottom depth exceeded the greatest depth sorting shell. An arithmetic mean was calculated for each cell of the triangular matrix. The cell means were averaged by row to yield an average vertical profile of fish density. Overall mean density was obtained by taking a mean of the vertical profile weighted for the thickness of the depth sorting shells.

At Nanticoke, apart from a limited area near the outfall, temperature was homogeneous horizontally and vertically, so only mean temperature during a census was calculated.

At Douglas Point composite temperature profiles for offshore locations were calculated when possible. Elevated temperatures were only obtained in the surface layer and thus plume temperatures are directly unimportant to fish counted acoustically in the 3–20-m layer. Apart from surface elevations of temperature near the outfall, there was no difference between inshore and offshore temperature profiles.

Results

NANTICOKE

Fish density varied considerably, though densities were generally low in the spring compared with the fall.

TABLE 1. Summary of environmental and fish abundance data obtained for each census at Nanticoke, 1974.

Census event 1974		Surface temp	Integrated[a] mean density/	Mean density/10 000 m³ by depth sorting shells (m)										
Day	Hour	(°C)	10 000 m³	3.0	4.5	7.0	10.5	16.0						
				↓	↓	↓	↓	↓						
Nanticoke														
Apr. 29	1130	8.1	861		4 020	125	33	0						
May 2	1145	8.6	237		849	129	53	0						
						6.7	10.0	15.5						
						↓	↓	↓						
10	1115	8.2	332		1 392	83	16	0						
						6.5	9.5	15.0						
						↓	↓	↓						
21	1045	11.8	162		525	105	18	0						
June 3	1045	11.8	218		332	167	195	0						
	P.M.	13.2	181		450	95	104	0						
6	—	15.6	14 204		43 428	8 765	3 218	0						
26	1110	15.6	184		200	143	203	0						
	1935	16.9	339		526	412	196	0						
	2245	16.4	832		2 632	423	204	0						
					4.0	5.0	6.0	7.0	8.0	10.0				
					↓	↓	↓	↓	↓	↓				
Sept. 9	1355	19.5	1 107		2 127	576	1 160	819	946	1 059				
10	0935	19.5	2 644		9 785	4 225	3 748	557	195	0				
	1930	20.0	1 947		4 696	3 218	2 091	1 340	1 006	640				
	2140	20.0	5 911		15 906	10 018	6 533	3 763	2 242	1 459				
18	1010	16.4	1 074		2 759	1 451	927	640	618	563				
											15.0			
Oct. 25	1320	11.4	740		2 225	396	413	359	303	742	↓			
28	1140	10.3	225		129	138	97	83	85	134				
											10.0			
Sandusk Creek											↓			
Sept. 18	1925	—	4 346		7 026	5 932	5 642	3 640	2 961	2 610				
											15.0			
Oct. 28	0950	—	26		44	42	13	42	10	16	↓			
Young's Creek														
Sept. 18	1650	—	61		40	89	240	11	24	13				

[a]Vertically integrated density 3–10 m.

TABLE 2. Summary of gillnet (+) and trap-net (*) fish catches at Nanticoke, 1974. (After Teleki 1976.)

Species	Apr. 25*	May									Sept. 10*	Oct. 25+
		2*	2+	8+	10*	21*	23*	26+	26*	27*		
Yellow perch	92	63	13	44	195	77	49	87	23	5	6	10
Rock bass	5	16	—	1	77	84	42	—	34	8	1	2
Freshwater drum	17	—	—	—	1	9	7	—	—	—	—	—
White sucker	5	—	—	5	9	1	2	—	—	—	—	—
Alewife	—	—	2	2	—	—	—	78	—	—	—	—
Other species	4	2	4	9	7	2	6	5	5	1	45	37
Total	123	81	19	61	289	173	106	170	62	14	52	49

Fish density usually decreased with increasing depth (Table 1). In the spring there were few fish present adjacent to the bottom. Yellow perch, *Perca flavescens*, predominated (Table 2 after Teleki 1976) in gillnet and trap-net catches. Rock bass, *Ambloplites rupestris*, though rarely encountered in gillnet captures, were often co-dominant with yellow perch in trap-net captures. Several other species were captured infrequently (Teleki 1976).

The horizontal distribution of fish was varied, as represented by densities in the 3–4- or 4.5-m depth shell (Fig. 1). In the spring (Fig. 1a, 2) fish appear to be aggregated inshore and/or over the more gently sloping bottom areas, though there was a marked prefer-

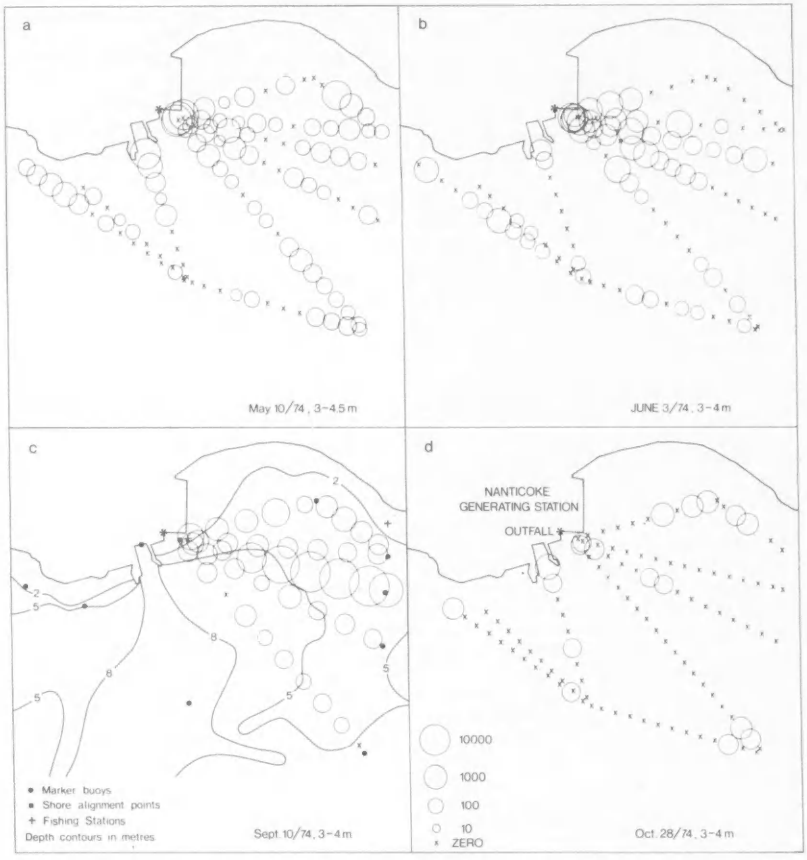

FIG. 1. Horizontal distribution of fish in the 3–4- or 4.5-m layer at the Nanticoke generating station, 1974.

ence for the outfall area. In the fall, when the plant was nonoperational, there was no evidence for any preference for the outfall area (Fig. 1c, d). The pattern observed on September 10 (Fig. 1c), when the fish were evenly distributed, might be characteristic of summer distribution. In late October (Fig. 1d) fish occurred in widely scattered clusters.

On two days, acoustic surveys were performed at different times of day: midmorning, evening, and at night. On June 26 and September 10 the highest densities were observed at night and the lowest were during the day (Table 1). The matrices suggest that density changes were brought about by offshore–inshore movements of fish but fish could also move from undetectable positions on the bottom up into the water column.

Since Kelso (1974, 1976a, b) indicated that water current may have an impact on fish behavior distinct from that induced by elevated temperatures, fish distribution at Nanticoke was compared with that at nearby river mouths on two occasions. Generally results (Table 1) indicated a response similar to that seen at the generating station but note that the two creeks have flow rates that average <1 m^3/s (Ongley 1976), considerably less than the Nanticoke discharge rate.

DOUGLAS POINT

Net captures consisted primarily of white sucker (*Catostomus commersoni*) longnose sucker and (*C. catostomus*), though the first set in May yielded a large catch of alewives (*Alosa pseudoharengus*) (Table 3). There was no consistent difference between the plume and control locations. The trend in catch sizes, apart from the large alewife catch, generally paralleled the densities observed by acoustic estimation. The high acoustic estimates in May appear to correspond with the presence of schools of alewife in the surface layers.

TABLE 3. Summary of gillnet fish catches at a plume (P) and control (C) site, Douglas Point, 1975.

Species	May 6		June 3		June 4		July 10		Aug. 3	
	P	C	P	C	P	C	P	C	P	C
Alewife	888	772	—	6	2	6	—	—	2	—
White sucker	8	13	17	28	13	10	10	5	1	23
Finescale sucker	18	19	22	10	24	11	4	2	3	4
Other species	2	2	2	6	4	2	5	2	11	4
Total	916	806	41	50	43	29	19	9	17	31

Daily mean fish density observed at Douglas Point showed little variation between sample dates, range of 108–310/10 000 m³. On August 25 a census performed at dusk gave a mean density of 671/10 000 m³. Densities were usually greatest in the shallowest depth shell and decreased with increasing depth (Table 4).

In late spring and early summer the horizontal distribution in the 3–4-m layer exhibited clustering. This was particularly noticeable inshore, where densities were highest in areas with relatively more gently sloping bottom, i.e. in front of the outfall and about 2 km south of the plant (Fig. 2a, b). The densest aggregations in this period were in front of the outfall. In the summer (July and August) fish were more evenly distributed (Fig. 2c), though the highest densities were still in the vicinity of the outfall. In September the trend appeared to be toward a more clustered distribution, as in the spring, with the highest density being observed near the outfall (Fig. 2d).

There was no strong relationship between the vertical distribution of fish and temperature structure (Fig. 3), though densities fall off more sharply with depth in the spring compared with the summer. The observation for August 7 is notable as on that day an upwelling event, a disturbance to the nearshore environment far larger than a thermal plume, pushed the thermocline to the surface. There was no perceptible change in the vertical distribution of fish, although the mean density for that day was the lowest observed.

Triangular matrices and Fig. 3 showed that the highest densities were usually in the 3–4-m layer, with cells near the bottom giving a secondary peak. The offshore midwater region normally had the lowest densities of fish. The matrix for August 7, during the upwelling event, exhibited the average pattern:

Depth Shell	Water depth (m) 3	4	6	8	10	15	20	>20
3	NS	815	811	859	625	632	191	
4		148	183	176	66	173	103	
6			655	83	87	25	11	
8				184	94	14	2	
10					150	64	0	
15						144	7	
20								

Since the same depth shells were used throughout the study at Douglas Point, a further analysis (after Johnson and Brinkhurst 1971) of the triangular matrices was possible (Table 5). The highest similarity values were generally with adjacent sampling dates and indicated a seasonal progression consistent with the seasonal pattern discerned (Fig. 3; Table 4) with respect to shifts in horizontal distribution.

Discussion

In an earlier study of fish distribution at the Pickering generating station, Lake Ontario (Kelso and Minns

TABLE 4. Summary of environmental and fish abundance data obtained for each census at Douglas Point, 1975.

Census event 1975		Water temp (°C)		Integrated[a] mean density/ 10 000 m³	Mean density/10 000 m³ by depth sorting shells (m)						
Day	Hour	0 m	20 m		3	4	6	8	10	15	20
					↓	↓	↓	↓	↓	↓	↓
May 7	0950	—	—	310	2478	760	571	294	69	24	
7	1450	—	—	255	2421	551	262	222	88	34	
8	1050	7.5	4.5	200	2394	342	159	117	39	34	
9	1000	7.5	4.5	155	1697	357	72	90	27	47	
Jun. 4	1020	13.5	5.0	155	1154	318	204	148	71	49	
July 7	1600	21.0	5.0	149	379	313	513	106	72	74	
Aug. 7	1000	14.0	5.5	108	656	142	172	73	71	76	
11	1520	18.5	11.0	190	577	105	111	83	414	110	
25	2050	—	—	671	4536	2350	1170	627	81	38	
26	1940	19.0	18.0	293	1519	962	713	267	55	39	
28	0920	19.0	8.5	211	690	183	643	376	123	92	
Sept. 16	1440	—	—	193	403	302	272	384	195	115	

[a]Vertically integrated density 3–20 m.

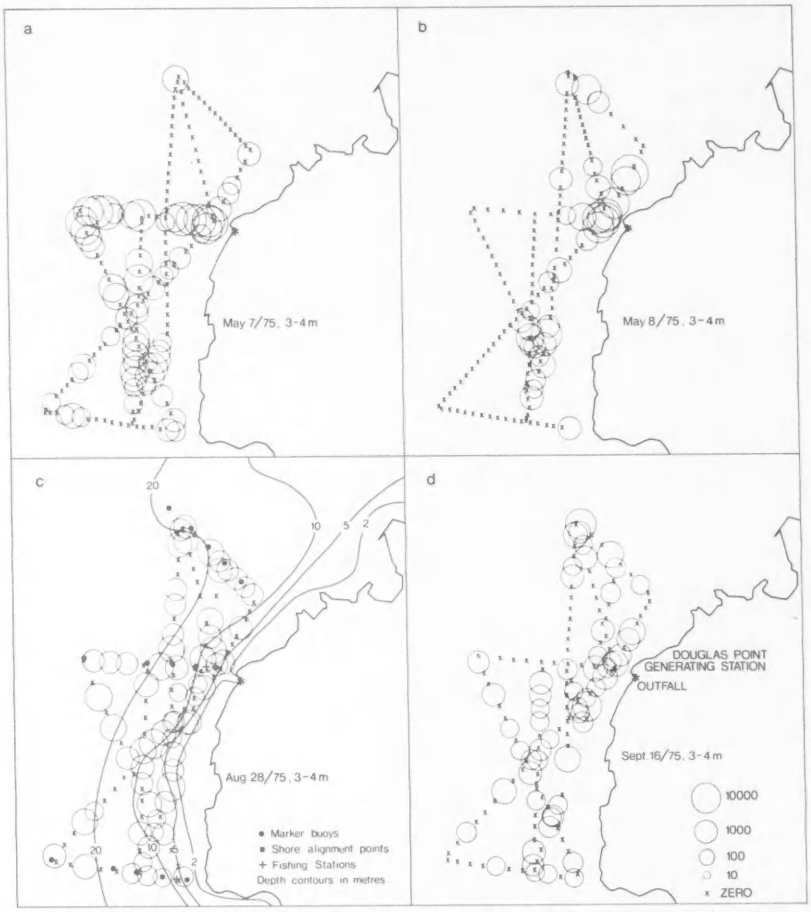

FIG. 2. Horizontal distribution of fish in the 3–4-m layer at Douglas Point, 1975.

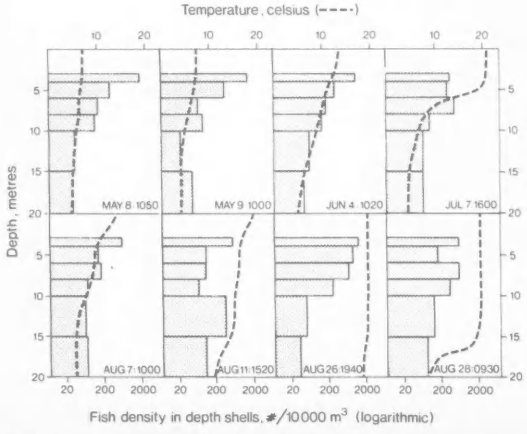

FIG. 3. Vertical distribution of fish in relation to temperature stratification at Douglas Point, 1975.

1975), the analysis centered on the thermal plume. In the present study thermal plumes were almost completely ignored for the following reasons. First, the studies at Pickering did not indicate any response by fish to plumes when the top 3 m were considered. Second, there were generally few fish in the 0–2- or 3-m layer as determined by a visual inspection of the echogram traces from Nanticoke and Douglas Point. Engel and Magnuson (1976) have made similar observations in Pallette Lake, Wis., using vertical gill nets and acoustic methodology. Similarly, Kelso (1976a) has observed only limited presence of fish into the 0–2- or 3-m layer using ultrasonic tracking of individual fish. Third, the thermal plumes at Nanticoke and Douglas Point were minimal since at Nanticoke the main discharge is tempered in the discharge canal and the volumes were small during our study and at Douglas Point the discharge volume is extremely small.

The attempt to identify indirect effects from thermal alteration inevitably becomes an attempt to unravel the

TABLE 5. Similarity of depth–depth-shell matrices of fish density among the censuses at Douglas Point.

	May 7, 0950	May 7, 1450	May 8, 1050	May 9, 1000	June 4, 1020	July 7, 1600	Aug. 11, 1520	Aug. 25, 2050	Aug. 26, 1940	Aug. 28, 0930	Sept. 16, 1440
May 7, 0950			*								
May 7, 1450	40.2		0	*	+	0	+	+	0		
May 8, 1050	76.7	56.3			0			0			
May 9, 1000	34.8	72.3	49.4		+		+	+	0		
June 4, 1020	36.3	69.0	51.4	69.0		0	+	*	+	0	0
July 7, 1600	34.5	51.8	41.6	48.6	59.6		0	0	+	0	0
Aug. 11, 1520	34.4	64.6	48.9	60.7	69.5	57.3		+	+	0	0
Aug. 25, 2050	46.6	66.6	51.4	60.9	70.8	55.3	64.5		*	+	+
Aug. 26, 1940	40.6	53.9	42.9	53.9	66.7	63.3	60.9	76.3		+	+
Aug. 28, 0930	33.3	47.6	36.5	34.6	50.2	55.4	56.7	61.1	64.9		+
Sept. 16, 1440	43.9	47.7	36.8	43.0	55.9	58.4	55.1	62.1	63.7	60.3	

1 — Similarity index based on $100 - 0.5 \sum |a_t^1 - b_t^1|$ (Johnson and Brinkhurst 1971)
$= \sum \min (a_t^1, b_t^1)$,
where a_t^1 = cell $a_t \times 100/\sum_1^n a_j$,
b_t^1 = cell $b_t \times 100/\sum_1^n b_j$,
n = # cells in matrix
a, b = fish abundance in cells.
2 — >70 ≡ *, 60–69.9 ≡ +, 50–59.9 ≡ 0, <50 blank.

complex interplay of factors influencing fish distribution. As temperature was not shown to be a determinant of vertical distribution of fish at either Nanticoke or Douglas Point, we took the opportunity to compare the depth distribution with incident radiation. At Nanticoke fish appeared to be deeper at higher light levels, while at Douglas Point the opposite response was apparent. The results can be partly explained by fish community redistribution within the acoustically surveyed space, by migration inshore of fish from midwater offshore, or by a movement upwards of fish from the layer bounding the bottom where fish are acoustically undetectable. Equally some fish could be moving deeper and/or offshore at night. Emery (1973) has observed, by diving, an offshore to inshore movement of fish at night but no evidence of any upward migration, though daytime schooling of many fish species was maintained at night. Evidently a more complete investigation of the influence of light is necessary.

The lack of a fish community response to temperature in their natural environment presents a sharp contrast to the well-established temperature preferenda and selection results derived from laboratory experimentation. At Nanticoke there was little vertical variation of temperature in the survey area and consequently no vertical response was to be expected. At Douglas Point there was thermal stratification present and there was no apparent response. Notably, there was no response to a massive disruption of the thermal regime in the form of an upwelling which pushed the thermocline to the surface (August 7). Fish density was slightly lower on that occasion but vertical distribution was unchanged. Fish in the natural environment may offset disadvantages due to temperature with advantages accrued via other factors, e.g. maintaining a proximity to preferred foods. However, it is also possible that the overall distribution of fish remains essentially the same, while habitat resource reallocation occurs on a species-specific basis. The laboratory-derived results would suggest that the latter hypothesis is more likely. However, laboratory experimentation on a species-specific preference is usually designed to minimize the interference of other factors.

Nonetheless, there is perceptible clustering of fish in the vicinity of thermal outfalls particularly in the spring and fall. The similarity of fish distribution at the Nanticoke outfall and at nearby tributary inputs suggest that turbulence may cause the clustering of fish. Kelso (1976a) showed that turbulence around the outfall, not temperature, affected fish movements at Nanticoke by comparing days when the generating station was discharging with and without a heat load. At Nanticoke and Douglas Point some clustering occurred at locations other than the outfall, usually in the area of shoals. The preference of fish for the outfalls of thermal generating stations may be a consequence of the turbulence regime and/or topographical irregularities, not the plume of elevated temperatures.

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Distribution and Disappearance of Radioactivity in Blood and Tissues of Coho Salmon (*Oncorhynchus kisutch*) After Oral Administration of ^{3}H-Testosterone

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FAGERLUND, U. H. M., AND J. R. MCBRIDE. 1978. Distribution and disappearance of radioactivity in blood and tissues of coho salmon (*Oncorhynchus kisutch*) after oral administration of ^{3}H-testosterone. J. Fish. Res. Board Can. 35: 893–900.

Yearling coho salmon (*Oncorhynchus kisutch*) were fed 3 times per day a diet containing 5 mg/kg of ^{3}H-testosterone until the concentration of radioisotope in all tissues was constant. Radioactivity was monitored in blood and 16 tissues for 10 d after the hormone was withdrawn from the diet. Excretion was via the hepatobiliary pathway. Sixteen hours after the last feeding of ^{3}H-testosterone, 93.1% of total radioactivity in soft tissues resided in the alimentary tract and gall bladder. Blood, skin, white muscle, and liver each contained about one fifth of remaining radioactivity. Concentrations of labeled substances in blood and testis were similar to or lower than normal androgen concentrations reported in salmonids. Ten days after steroid withdrawal concentrations were 1 ng/g or lower in all tissues.

Key words: salmonid, diet, anabolic effect, androgen, testosterone, half-life, radioactivity, residue, tissue

FAGERLUND, U. H. M., AND J. R. MCBRIDE. 1978. Distribution and disappearance of radioactivity in blood and tissues of coho salmon (*Oncorhynchus kisutch*) after oral administration of ^{3}H-testosterone. J. Fish. Res. Board Can. 35: 893–900.

Nous avons donné 3 fois par jour à des saumons coho (*Oncorhynchus kisutch*) de l'année une nourriture contenant 5 mg/kg de ^{3}H-testostérone jusqu'à ce que la concentration du radioisotope soit uniforme dans tous les tissus. Nous avons suivi la radioactivité dans le sang et dans 16 tissus durant une période de 10 jours après que l'hormone ait été supprimée du régime. L'excrétion se fit par voie métabolique hépato-biliaire. Seize heures après le dernier repas de ^{3}H-testostérone, 93.1% de la radioactivité totale dans les tissus mous se trouve dans le tractus digestif et la vésicule biliaire. Le sang, la peau, le muscle blanc et le foie contiennent chacun environ un cinquième de la balance de la radioactivité. Les concentrations de substances marquées dans le sang et le testicule sont identiques ou inférieures aux concentrations normales d'androgènes signalées chez les salmonidés. Dix jours après le retrait du stéroïde, les concentrations sont de 1 ng/g ou moins dans tous les tissus.

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ANDROGENS, both natural and synthetic, have anabolic properties when administered orally to salmonid fish (McBride and Fagerlund 1973, 1976; Fagerlund and McBride 1975, 1977; Simpson 1976; Cheema and Matty 1976; Yamazaki 1976; Higgs et al. 1977; Saunders et al. 1977).

Hormonal growth stimulation as a technique in the culture of salmon may be applied either to the rearing of juveniles in hatcheries or to the raising of fish to market size. In the former case, hormone residues in tissues of hatchery-reared juvenile fish released into waterways may affect other organisms inhabiting the aquatic environment. In either case the fish are ultimately used for human consumption. The concentration of hormone residues in the tissues of treated fish therefore becomes a matter of concern to the public. The present investigation was undertaken to estimate (1) the concentration of substances in blood and tissues of coho salmon resulting from the prolonged feeding of a dose of testosterone which induced growth and (2) the rate of disappearance of these substances after the hormone was withdrawn from the food.

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Materials and Methods

EXPERIMENTAL ANIMALS

The fish used in this study were yearling coho salmon (*Oncorhynchus kisutch*) with a wet weight of 40 ± 1.5 g ($\bar{x} \pm$ SE). As part of a separate study they had previously

been fed a commercial pelleted diet containing 5 ppm (5 mg/kg) of testosterone 3 times per day for 244 days (McBride and Fagerlund 1976) and, as a result of this prior treatment, the mean weight of the group was 24.7% greater than that of a control group fed a supplement free diet. Histological examination of gonads taken from the treated group did not reveal any androgenic effects of the hormone.

During the present study the 40 test fish were held under a natural photoperiod in an 850-L tank supplied with aerated running water at 5°C.

Administration of Labeled Steroid

One kilogram of Oregon moist pellets (OMP, Moore-Clark Corp., La Conner, Wash.), 3.18 mm diam ($\frac{1}{8}$ in.), were spread out over a 30 × 30 cm pan. Four millicuries (0.148 GBq) of 1,2,6,7-^{3}H-testosterone (New England Nuclear Corp., Boston, Mass., specific activity 85 Ci/mmol [3145 GBq/mmol]) and 5 mg of testosterone (Sigma Chemical Co., St. Louis, Miss.) were dissolved in 4 mL of 95% ethanol. Specific activity of testosterone in the solution was 576.9 dpm/ng (decompositions per minute/ng). The solution was sprayed over the pellets with a chromatogram sprayer delivering a fine spray. During spraying the pellets were mixed with a spatula. The sprayer was rinsed with 1 mL of 95% ethanol, which was also sprayed on the pellets. Finally, the pellets were thoroughly mixed in the pan. Purity of ^{3}H-testosterone was checked by thin-layer chromatography in benzene–acetone (4:1). Three times a day, 0830, 1130, and 1600, the diet containing labeled testosterone was fed to the fish in small portions until the fish rejected the pellets. The feeding was continued for 10 d. On the 11th d and thereafter, fish were fed OMP without added hormone.

Sampling of Fish

Four fish were taken at 0800 before the first meal of the day as follows: 1, 2, 3, and 6 d after feeding the treated diet had commenced and 1, 2, 3, 6, and 10 d after the hormone was withdrawn. The fish were immobilized by rapid and deep anesthesia in 2-phenoxyethanol (2 mL/L) (Eastman Kodak Co., Rochester, N.Y.). The tail was severed at the caudal peduncle and 0.10 mL of blood was collected with a heparinized tube and placed in a glass scintillation vial. After the fish had bled for 10 min they were wrapped in aluminum foil. Fish and scintillation vials were then frozen.

Tissue samples were excised from weighed, partially thawed fish in the following manner:

Muscle	100–150 mg	Dorsal, anterior to dorsal fin
Gill	20– 50 mg	The first gill arch with attached gill rakers
Kidney	20– 50 mg	Midsection
Liver	50–100 mg	Slice
Pyloric ceca	50–100 mg	Several appendices
Small intestine	50–100 mg	Anterior segment

The following organs were taken in toto: ovary, testis, brain including pituitary, spleen, gall bladder, and head kidney. All samples of the alimentary tract were taken with contents included, and gall bladders were taken intact.

Tissue and blood samples were digested in preweighed scintillation vials, with 1 mL of Protosol® tissue solubilizer (NEN Canada Ltd., Lachine, Quebec).

Total radioactivity in tissues was calculated during isotopic equilibrium, defined as a state, reached by continuous administration of an isotope, during which the concentration of isotope is at its highest and constant level in all tissues (Jacoby and Hickman Jr. 1966). For this purpose gill tissue from one side of the fish and heart, kidney, liver, stomach, pyloric ceca (with adjoining part of large intestine), and small intestine were excised in toto from the four fish taken after receiving labeled testosterone for 6 d. After weighing, these tissues were digested in the appropriate amount of Protosol®. A 1-mL sample of each digest was removed for scintillation counting. From these same fish the skin from one side was separated from the muscle, the muscle was scraped off the backbone, and skin and muscle samples were weighed. From the other side of each of these fish, in the dorsal area and anterior to the dorsal fin, a sample of skin and a piece of muscle around the lateral line consisting mainly of adipose tissue (~ 40 mg each) was removed and digested. The samples of adipose muscle made up $\frac{1}{10}$ of the weight of the total muscle in the section. The muscle and skin samples were assumed to be representative of the total of those tissues for the purpose of this study. The volume of blood removed by bleeding the fish was assumed to be 3% of weight of soft tissues (Smith 1966).

Ten millilitres of a toluene-based scintillation fluid was added to all digests. To depress quenching, 5-mL aliquots (from a total of 11.1 mL) of cocktails containing blood were further diluted with 5 mL of scintillation fluid. Once excessive counts caused by chemoluminescence had subsided, radioactivity was determined in a Packard scintillation counter. Quenching was determined from a curve drawn with the aid of a set of quench standards. The effect of quenching was also checked by adding a known amount of labeled testosterone to cold digests of all tissues.

Regression lines for radioactivity of tissues (dpm/g) vs. time were calculated by the method of least squares. From the slopes (k) of the regression lines half-lives ($t^{\frac{1}{2}} = 0.693 \div k$) were obtained.

Results and Discussion

Uptake and Disappearance of Radioactivity

Metabolic products of testosterone were not separated and identified in this investigation. Consequently it is not possible to determine from our data the portion of the ingested steroid that remained unchanged. Metabolism of the testosterone molecule in mammals results in modification of functional groups and unsaturation of the nucleus (Dorfman and Ungar 1965). The metabolism of testosterone in salmonids has received scanty attention. Metabolites isolated so far are similar to those in mammals (Ozon 1972). An exception is the formation of C^{11}-oxygenated steroids, which has been documented in testes of Atlantic salmon (*Salmo salar*) (Idler and MacNab 1967). In liver of rainbow trout (*S. gairdneri*) testosterone was metabolized to 5α- and 5β-androstanes in microsomal and cytoplasmic fractions, respectively (Lisboa and Breuer 1966). A high metabolic activity was demonstrated by Hay et al. (1976) in 2-h incubations with skin of rainbow trout (*S. gairdneri*), which converted 13.34% of testosterone to 5α-dihydrotestosterone, while only 0.75–3.0% was

TABLE 1. Concentration of labeled substances in tissues (ng/g) calculated from radioactivity data. Molecular weight of metabolites was assumed to be equal to that of testosterone.

	Isotopic equilibrium (2–6 d of feeding)			10 d after steroid was withdrawn		
	Mean	SE	No. of fish	Mean	SE	No. of fish
Blood	5.93	1.28	12	<0.11		4
Skin	1.88	0.59	4	—	—	—
White muscle	0.41	0.06	12	<0.06		4
Dark muscle	0.65	0.25	4	—	—	—
Gill	2.64	0.55	12	<0.09		4
Testis	9.80	3.30	5	<0.80		3
Ovary	6.48	2.71	7	0.03	0.03	3
Kidney	4.40	0.87	12	0.11	0.07	4
Head kidney	3.13	0.69	12	0.07	0.07	4
Brain	1.92	0.26	12	0.06	0.02	4
Spleen	1.62	0.42	12	0.13	0.13	4
Heart	4.46	1.03	4	—	—	—
Liver	13.35	2.79	12	0.23	0.03	4
Gall bladder	2392.00	307.00	11	1.00	0.30	3
Stomach	39.69	20.45	4	—	—	—
Pyloric ceca	137.00	44.38	12	0.51	0.15	4
Small intestine	392.00	82.68	12	0.52	0.12	4

converted by muscle. Only small amounts of other metabolites were derived from skin and none from muscle. Small amounts of testosterone were recovered from the glucuronide fraction from both tissues.

We assumed that the samples of muscle and skin, although taken from localized areas of the body, were representative of the total muscle and skin mass. Hay et al. (1976) found that the patterns of steroid metabolism were similar in dorsal and ventral skin, and also in dorsal skin from male and female adult and immature rainbow trout. Most of the metabolism occurred in the dermis and only a small fraction in epidermis.

There was no apparent increase in radioactivity of blood or tissues in samples taken after 1, 2, and 3 d of feeding labeled testosterone, indicating that isotopic equilibrium was reached in all parts of the body within 24 h after test feeding had commenced. To arrive at an estimate of the total concentrations of labeled steroids in tissues during isotopic equilibrium (Table 1), testosterone and metabolites were assumed to have identical molecular weights. This assumption introduces some errors into the tissue concentration data, mainly because unknown proportions of the steroids are conjugated with glucuronic acid and probably sulphuric acid and the proportions vary from tissue to tissue (Grajcer and Idler 1961, 1963; Schmidt and Idler 1962; Hay et al. 1976). Sixteen hours after the last test meal of the day the concentration of labeled substances in blood was 5.93 ng/mL when calculated under this assumption. The concentration in the gall bladder, the organ with the highest radioactivity per gram, decreased from 2392 to 1 ng/g within 10 d after steroid withdrawal. The 16-h concentration in blood was within the

TABLE 2. Half-life of radioactivity in tissues after withdrawal of steroid from the diet.

Tissue	Days after withdrawal	$T_{\frac{1}{2}}$ (h)
Blood	0–3	11.16
White muscle	0–3	13.90
Gills	0–3	13.80
Testis	0–3	11.16
Ovary	0–2	9.61
Kidney	0–3	10.80
Head kidney	0–3	11.47
Brain	0–3	24.20
	3–10	74.64
Liver	0–3	17.12
	3–10	147.40
Gall bladder	0–6	14.44
	6–10	61.86
Pyloric ceca	0–6	23.31
	6–10	52.47
Small intestine	0–6	20.68
	6–10	40.75

range of the physiological concentration of androgens noted by Schreck et al. (1972a) in plasma of castrated male (6.8 ng/mL) and female (4.8 ng/mL) rainbow trout. Before castration the values were considerably higher, namely 27.4 and 13.2 ng/mL in males and females, respectively. Schreck et al. (1972b) reported androgen levels ranging from 20 to 110 ng/mL in plasma of 2-yr-old spawning rainbow trout. There was a strong correlation between gonadosomatic index and plasma androgen concentrations in both male and female trout. Grajcer and Idler (1963) found 154 ng/mL of testosterone present as free steroid and glucuronide in plasma and 32.5 ng/g of testosterone glucuronide in testis of adult sockeye salmon (*O. nerka*). During sexual maturation androgen levels in testes increased in this species from the equivalent of 41 ng testosterone propionate to 133 ng/g (Idler and Tsuyuki (1959).

The concentration of radioactivity in skin (1.88 ng/g) was high, considering the poor vascularization of the tissue. This observation, together with the high rate of steroid conversion in skin reported by Hay and coworkers, suggests that skin of salmonids is an important target organ for androgens. This agrees with the findings of McBride and van Overbeeke (1971) that gonadal hormones increase the thickness of the skin of gonadectomized sockeye salmon (*O. nerka*).

There is no indication in the literature that testosterone administered to vertebrates forms metabolites that are different from those occurring naturally. Consequently, each radioactively labeled metabolite, when entering body fluids and tissues, mixes with its endogenous counterpart and thereby increases the concentration of that metabolite. It is likely that the rate of excretion of isotope, when carried by the increased concentrations, is higher than when labeled testosterone

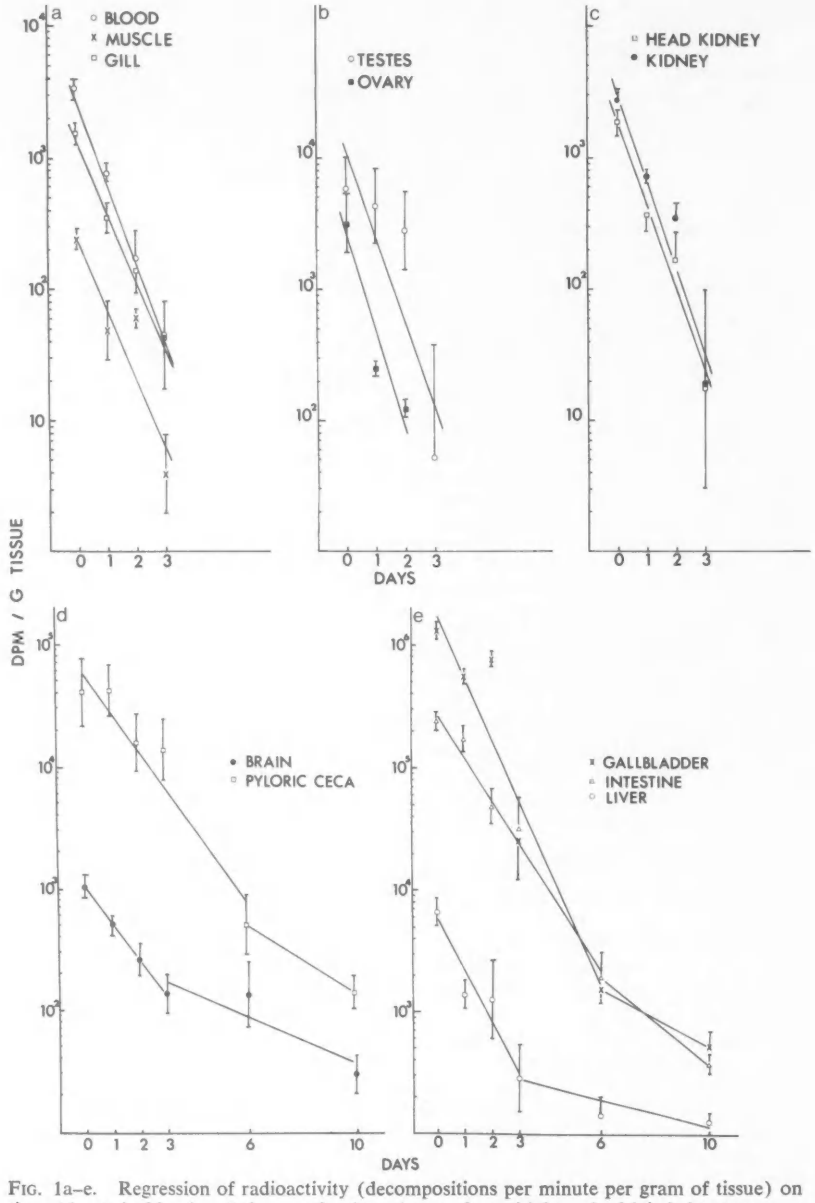

FIG. 1a–e. Regression of radioactivity (decompositions per minute per gram of tissue) on time (days) in blood and tissues of coho salmon after withdrawal of labeled testosterone from the diet.

is administered in a trace amount, as is the normal procedure when studying steroid kinetics. The half-lives which we calculated (Table 2) are therefore useful mainly for comparing secretion rates between blood and tissues.

The radioactivity of blood, white muscle, gill (Fig. 1a), testis, ovary (Fig. 1b), kidney, and head kidney (Fig. 1c) decreased exponentially during the first 3 d after termination of ^{3}H-testosterone feeding and, with the exception of an occasional single fish, was not de-

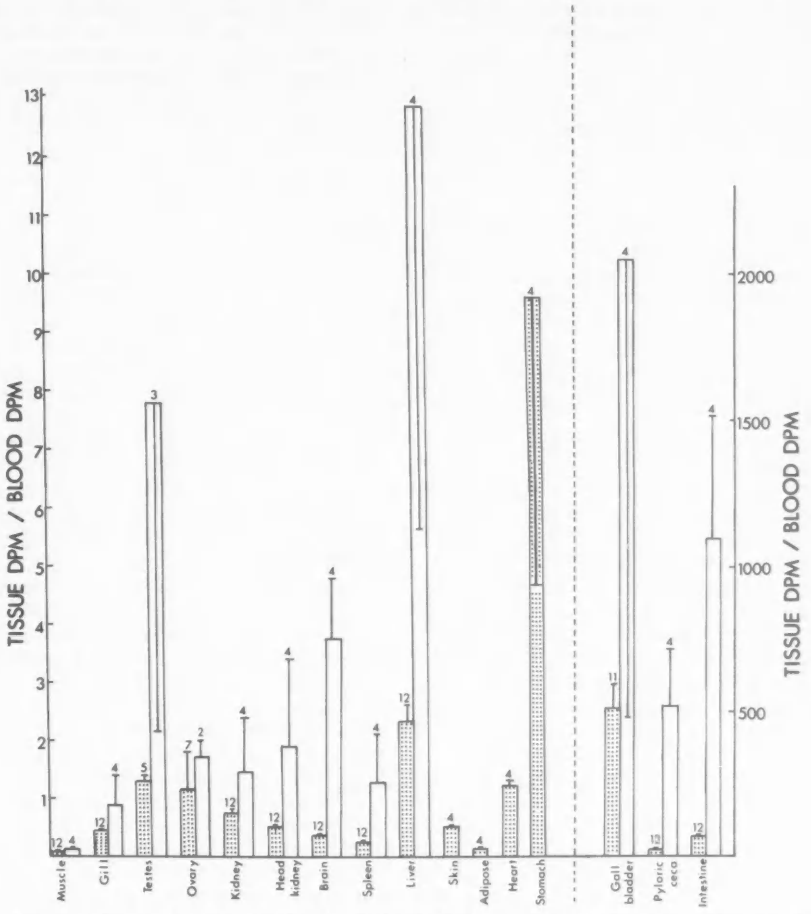

FIG. 2. Tissue to blood ratio of radioactivity during isotopic equilibrium (dotted bars) and 3 d (for ovary 2 d) after labeled testosterone was withdrawn from the diet (unshaded bars). Vertical lines denote ±SE. Figures above bars denote numbers of fish.

tectable after 6 d. If a higher specific activity of administered ^{3}H-testosterone had been chosen, radioactivity may have been detected in these tissues after day 3. The half-lives in these tissues (Table 2) were similar to each other. They were shorter than those in brain, liver, gall bladder, pyloric ceca, and small intestine. Labeled substances disappeared from blood with a half-life of 11.2 h. Only one investigation has been reported in the literature in which the clearance rate of an androgen in blood of fish was investigated by using tracer amounts of labeled steroids. Schreck (1973) injected labeled testosterone into the epaxial muscle of yearling rainbow trout (*S. gairdneri*) and found half-life of radioactivity in plasma to be 2.5 h when measured within 24 h of an injection, a period during which the injected hormone is rapidly dispersing throughout fluids and tissues of the body causing the initial half-life to be short. A short half-life in blood may also be expected when the radioactivity is delivered in a single injection, since uptake into tissue binding sites from blood is less extensive than during isotopic equilibrium. Schreck did not find a difference in plasma half-life between sexes. Also, in the present study sex differences were not obvious in respect of any tissue except gonads. However, statistical analysis of possible sex differences was not attempted, since numbers of fish of either sex were small and ranges of values large.

Half-life in testis was identical to that in blood. Nevertheless, testis to blood ratios (Fig. 2) increased from 1.28 ± 0.15 (SE) on day 0 to 5.29 ± 3.13 on day 1, 8.13 ± 4.35 on day 2, and 7.7 ± 5.61 on day 3. The tissue–blood data indicate preferential uptake of radioactivity in this organ. The contradiction between half-

lives and testis to blood ratios may be explained by the fact that, while obviously only male fish were included when calculating testis radioactivity, blood radioactivity was calculated using both male and female fish. Consequently the testis–blood data, which are means of ratios for individual fish, are more reliable when relating testis to blood radioactivity. This applies also to the comparison between ovary and blood. Half-life of radioactivity (9.61 h) in ovary and the high tissue to blood ratio at isotopic equilibrium (1.16 ± 0.44), which was slightly lower than the corresponding values for testis, indicate tissue uptake also in this organ. However, the increase in the ratio was not of the same magnitude as in testis. The values were 0.43 ± 0.03 on day 1 and 1.73 ± 0.35 on day 2. In Schreck's (1973) study on rainbow trout the half-life of radioactivity was considerably longer in testis (23 h) than in ovary (7 h) and liver (8 h).

Radioactivity in spleen fluctuated over a wide range making the calculation of half-life meaningless.

Disappearance of radioactivity from the brain was biphasic (Fig. 1d). This was the only tissue, with the exception of those on the excretory pathway, in which radioactivity persisted between days 3 and 10. Half-life in 3–10 d (74.6 h) was longer than in any tissue except liver (147.4 h). The brain to blood ratio increased steadily (Fig. 2) after hormone withdrawal. A possible cause of the slow disappearance may be tissue-binding of either testosterone or a metabolite. Protein-binding of androgens in brain has not been previously reported in fish. In mammals hypothalamus and pituitary are target organs for androgens (McEwen et al. 1972).

The disappearance of radioactivity from pyloric ceca (Fig. 1d), liver, gall bladder, and intestine (Fig. 1e) followed a biphasic pattern. During the first 3 or 6 d the half-lives were in the range of 20 h, but they increased considerably during subsequent days. The tissue to blood ratios of radioactivity (Fig. 2) at isotopic equilibrium for liver (2.36) and gall bladder (505.9) demonstrate that these organs form the principal route of excretion. Schreck (1973) also found evidence for hepatic elimination in rainbow trout.

Implications for Public Health

When hormonal growth promoters are used in the culture of food fish, the amounts of administered hormone and its metabolites residing in tissues should not be as high as to be a hazard to the consumer. The main purpose of this study is to provide information regarding length of drug withdrawal time required for tissue residues to decrease to levels acceptable from the point of public health.

Testosterone was not separated from metabolites in this study and therefore data obtained relate to the sum of testosterone and its metabolites. The purpose of the study is served by this approach since many of the metabolites of testosterone have physiological effects in man (Jones 1977).

Table 3. Distribution of radioactivity in tissues of four fish after ingestion of ^{3}H-testosterone to isotopic equilibrium. A, Tissue decompositions per minute in percent of total dpm of all sampled tissues; B, tissue dpm in percent of total dpm of sampled tissues excluding alimentary tract and gall bladder.

	A		B	
Tissue	Mean	SE	Mean	SE
Blood	1.34	0.11	20.47	2.73
Skin	1.65	0.14	22.39	3.39
White muscle	1.35	0.24	19.74	1.81
Dark muscle	0.33	0.09	4.65	0.94
Gill	0.38	0.04	5.26	0.57
Testis / Ovary	0.019	0.002	0.30	0.05
Kidney	0.159	0.028	2.34	0.32
Head kidney	0.050	0.007	0.74	0.06
Brain	0.066	0.009	1.03	0.19
Spleen	0.005	0.001	0.09	0.03
Heart	0.064	0.111	0.93	0.06
Liver	1.51	0.22	22.01	1.28
Gall bladder	15.34	4.35		
Stomach	4.82	2.57		
Pyloric ceca	37.60	4.57		
Small intestine	35.32	2.99		

Testosterone is an endogenous steroid in coho salmon and the administered steroid and metabolites may be assumed to mix with the endogenous pool. The results presented here, however, relate to the steroids of exogenous origin. Because of variations in the rates of feed intake, absorption and metabolism radioactivity data for individual fish vary over a large range and the data provided here should be regarded as approximations.

When food containing 5 mg/kg of labeled testosterone was fed for some time to juvenile coho salmon and samples were taken 16 h after a previous meal, the stomach, pyloric ceca, gall bladder, and intestine combined contained 93.1% of total radioactivity in soft tissues (Table 3). The major portion of remaining radioactivity was distributed equally between blood, skin, white muscle, and liver. If a daily food intake of 3% of body weight is assumed, the mean total radioactivity in all soft tissues was 6.1% of the amount ingested during the previous 24 h. Expressed as steroid concentration a daily intake of about 150 ng of testosterone per gram of fish resulted in a soft tissue concentration of 9.15 ng/g.

Anabolic steroids may be administered during hatchery rearing of juvenile salmon to increase the size at the time the fish become ready for seaward migration (McBride and Fagerlund 1976). For coho the rearing time is normally 15 mo. After the fish are released they do not become available for human consumption until after several months of ocean life, when a small percentage of the fish return to the river, from which they were released. Our results indicate that after this length of time the combined concentrations of androgens of

endogenous and exogenous origin are indistinguishable from normal endogenous levels. The majority of adult coho return after more than 1 yr in the ocean. After being released from the hatchery, treated fish may be consumed by larger fish. The recipient fish, assumed to consume 5% of its body weight, may feed entirely on hormone-treated smolts. Any hormone residue present in the released fish will be diluted in the body of the recipient fish to 5% of the concentration in the smolts on the basis of size alone. Further dilution takes place through metabolic activity in the recipient fish. Such a fish may be caught immediately after having fed on hormone-treated fish. If the fish is used for human consumption the intestines, in which most of the residual, originally administered hormone and its metabolites reside, are usually removed. Because of the dilution of the originally administered steroid, it would appear that testosterone-treated smolts may safely be released from a hatchery without being subjected to a withdrawal period, even if all the hypothetical events outlined above were to take place.

Anabolic hormones may also be used in the culture of fish reared for immediate marketing such as rainbow trout. Our data, although relating to much smaller fish, may be used as a general guideline to assess tissue residues in these fish. Fish to be taken either as pan-sized (~ 300 g) or as adult fish (500 g or larger) are generally marketed after intestines, including the kidney and gills, have been removed. Sixteen hours after a previous meal the remaining soft tissues, skin, and muscle (with blood included since fish are not always bled at time of killing) would contain less than 5% of total steroids of exogenous origin in the body. We found that the concentration of exogenous steroids in blood (5.93 ng/g) was less than normal androgen concentrations reported in blood of salmonids. Physiological concentrations in skin and muscle of salmonids have not been determined but are probably also higher than the 16-h concentrations reported here, since tissue distribution of endogenous androgens may be assumed to be similar to the distribution of nearly physiological levels of exogenous androgens. Consequently a hormone withdrawal period of 1 wk before processing appears to be ample to ensure the absence of hormone levels detrimental to public health.

The results we have obtained are not necessarily applicable to other species, particularly those belonging to other orders or classes, since differences in metabolic rate may occur. For instance, Hay et al. (1976) observed considerable quantitative differences between rainbow trout (*S. gairdneri*) and spur dogfish (*Squalus acanthias*) in production of metabolites when testosterone and androstenedione were incubated with muscle or skin homogenates.

The duration of the withdrawal period, particularly for marketable fish, will ultimately be decided in consultation with national health authorities. Factors influencing the decision will include the rate of clearance from tissues, the properties of the hormone, as regards toxicity and carcinogenesis, and the anticipated effectiveness of enforcement of withdrawal periods.

Acknowledgments

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Alternative Sampling Device for Aquatic Organisms

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BRODIE, P. F. 1978. Alternative sampling device for aquatic organisms. J. Fish. Res. Board Can. 35: 901–902.

Problems of obtaining quantitative samples of aquatic organisms via conventional devices are discussed and an alternative sampler based on the presumed mechanics of cetacean feeding is proposed. A polyethylene tube mounted on a light frame that minimizes the bow wave envelops a column of water and permits its filtration.

Key words: avoidance, bow wave, plankton, quantitative sample, sampler, turbulence, water column

BRODIE, P. F. 1978. Alternative sampling device for aquatic organisms. J. Fish. Res. Board Can. 35: 901–902.

L'auteur analyse les problèmes associés à la collecte d'échantillons quantitatifs d'organismes aquatiques au moyen d'appareils conventionnels et propose un autre échantillonneur dont le principe repose sur ce qu'il suppose être le mécanisme d'alimentation des cétacés. Un tube de polyéthylène fixé sur un cadre léger causant un minimum de vague de proue enveloppe une colonne d'eau de façon à permettre sa filtration.

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MAJOR problems arise in plankton sampling when water is filtered while it is being collected. The size of the mesh is not really an indication of the porosity since each fiber has a boundary layer and a bow wave. If the device is not a cylinder or a frame with parallel sides there are pressure differentials that cause it to sample either more or less of the cross section of the frame. Small particles either pass or are forced through the filter by the water pressure. Thus conventional sampling devices are forever hindered by turbulence and by being visible and probably audible to some organisms. The result is that they are not quantitative.

If a column of water could be enveloped by a sampler with minimal bow wave the problems outlined above could be overcome. In addition, if one could be certain of the length of the water column enclosed, quantitation would be greatly improved. This note describes such a device.

Alternative sampler — To construct a sampling device capable of satisfying the requirements of reduced bow wave and accurate sample volume, we began with a cylinder of sheet metal and attached to this a hydrofoil handle (Fig. 1). This frame will pass through the water fairly cleanly. From the back of the frame we wish to extrude a fine sheath that will envelop a column of water.

Any material that could be stored on the back of the frame is necessarily thin and delicate. Fine polyethylene tubing such as that used for dry-cleaning bags is suitable for such a device. This material is available in continuous rolls and is inexpensive. It is nearly invisible underwater and when loaded on the frame with one end either tied or heat sealed gives the impression, underwater, of a cylinder open at both ends; this possibly reduces the escape reaction by organisms.

The sheath is so sensitive to movement that during lab experiments the sheath on a 40 cm diam cylinder payed off as the frame moved slowly through the air. The ease with which the sheath pays off increases as a longer column, with greater inertia, is enclosed. The problem of moving the frame without triggering the sheath could be solved by removable end covers.

Any sample greater than a few litres is difficult to manage unless lifting equipment is available. If, however, the captured water column (up to several thousand litres) need never be removed from the water surface, lifting equipment and a large working platform wouldn't be necessary. Once the sheath is fully extruded, arrangements must be made to avoid tearing the sheath. This can be accomplished by (1) having the mouth of the frame break the water surface, or (2) detaching the

[1]Bedford Institute of Oceanography Contribution.

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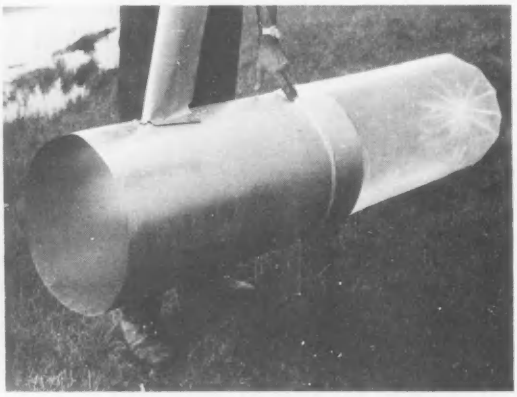

FIG. 1. Prototype sampler of 40 cm diam made from sheet metal with a polyethylene (dry-cleaning bag tubing) sheath several metres long. Note that the sampler is activated and must be restrained in a light breeze.

enclosed water cell from the frame at the point of maximum extrusion by pursing the end with a light drawstring.

Once the water column is isolated it is processed by attaching a filter to one end and pulling the other end out of the water at a speed that allows evacuation through the filter.

The device is probably not as easily detected by its bow wave or by noise, but it might be seen. Experimental work has indicated that the frame is under very little stress and can be made from thin acetate or acrylic. For larger, metal frames a clear tube can be mounted at the leading edge to envelop organisms before they detect the frame.

Such a sampler can be used for horizontal or vertical sampling from small boats or used by divers since little power is required. Collars of acetate or metal can be loaded with several metres of polyethylene and set on the bottom of shallow areas. These can be pulled to the surface with fine monofilament lines. The small bubbles trapped in the folds when the frame is loaded will act as flotation. A heavy, glass disk or filtering apparatus set in the bottom of the sheath will keep the frame on the bottom until manually pulled up.

Smaller models can be used to sample laboratory aquaria. In this case the sheath is taped to the frame allowing the frame to be raised above the surface for vertical sampling. Organisms can be captured, examined, or counted while the "cell" lies on the surface, then returned to the tank with minimal damage to the organisms and without reducing the aquarium population.

Frames need not be circular but could be compressed oval shaped to sample narrow layers close to the surface or bottom.

The advantages of this system are that the materials are inexpensive, readily available, and can be constructed easily. Polyethylene tubing is readily available in a variety of sizes and thicknesses. Costs are very low unless special dimensions require low production runs by the manufacturer.

The device described here is delicate and the procedure sometimes laborious, thus its value may be more as a calibration device for other, more rugged samplers.

The design of this sampler resulted from morphological studies of rorquals (baleen whales with highly expandable throat pouches) and the presumed mechanics of their feeding apparatus when engulfing highly concentrated prey (Sutcliffe and Brodie 1977, fig. 2; Brodie 1977).

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Viral Erythrocytic Necrosis: Natural Occurrence in Pacific Salmon and Experimental Transmission

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EVELYN, T. P. T., AND G. S. TRAXLER. 1978. Viral erythrocytic necrosis: natural occurrence in Pacific salmon and experimental transmission. J. Fish. Res. Board Can. 35: 903–907.

A necrotic disease of erythrocytes of chum (*Oncorhynchus keta*) and pink (*O. gorbuscha*) salmon is described at the light and electron microscopic level. The disease is characterized by a single cytoplasmic inclusion in affected erythrocytes and by the presence of an associated intraerythrocytic virus probably belonging to the icosahedral cytoplasmic deoxyribovirus (ICDV) group. Isolation of the virus was unsuccessful, but viral etiology was implicated by inoculation of chum and pink salmon using filtered preparations from diseased specimens of the former. Chinook (*O. tshawytscha*), coho (*O. kisutch*), and sockeye (*O. nerka*) salmon proved refractory.

Key words: viral disease, Pacific salmon, blood, erythrocytes, anemia

EVELYN, T. P. T., AND G. S. TRAXLER. 1978. Viral erythrocytic necrosis: natural occurrence in Pacific salmon and experimental transmission. J. Fish. Res. Board Can. 35: 903–907.

On décrit dans cet article une maladie nécrosante des érythrocytes de saumons keta (*Oncorhynchus keta*) et roses (*O. gorbuscha*) à partir d'observations aux microscopes photonique et électronique. La maladie est caractérisée par une seule inclusion cytoplasmique dans les érythrocytes affectés et par la présence d'un virus intraérythrocytique associé appartenant probablement au groupe désoxyribovirus cytoplasmique icosaédrique (ICDV). Les tentatives d'isolation du virus ont échoué, mais il a été possible de déterminer l'étiologie virale par inoculation dans des saumons keta et roses en faisant appel à des préparations filtrées provenant de saumons keta atteints de la maladie. Les saumons chinook (*O. tshawytscha*), coho (*O. kisutch*) et nerka (*O. nerka*) se sont avérés réfractaires.

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PISCINE erythrocytic necrosis (PEN) was the term used by Laird and Bullock (1969) to describe an abnormal condition in three species of marine fishes taken from the Atlantic Ocean off eastern North America. The condition was characterized by the presence of an inclusion body in the cytoplasm of affected erythrocytes, and was clearly pathological in the Atlantic cod (*Gadus morhua*). Laird and Bullock encountered PEN during a study of marine fish hematozoa and although uncertain of its etiology, they were aware that it might be viral. Subsequently, other workers confirmed that PEN in cod was virus-associated (Walker 1971; Appy et al. 1976; Walker and Sherburne 1977). In section the virus appeared as a large, hexagonal, cytoplasmic particle and was similar to viruses in the icosahedral cytoplasmic deoxyribovirus (ICDV) group of Kelly and Robertson (1973). A similar virus-associated erythrocytic condition was also reported in the blenny (*Blennius pholis*) collected in the North Atlantic off the Welsh coast (Johnston and Davies 1973), and it seems likely that the disease in other poikilothermic vertebrates will, in many cases, also prove to be viral. For example, infections with ICDV-like viruses were found in three of five PEN-like cases recently investigated by electron microscopy. While the condition in dogfish (*Scyliorhinus canicula*) and Atlantic mackerel (*Scomber scombrus*) was due to uncertain and to protozoan etiology, respectively (Johnston 1975), that in the gecko (*Gehyra variegata*) (Stehbens and Johnston 1966), the leopard frog (*Rana pipiens*) (Bernard et al. 1968), and the Atlantic herring (*Clupea harengus harengus*) (Sherburne 1973; Reno et al. 1978) was virus-associated.

The purpose of our report is to record and describe erythrocytic necrosis (EN) in a new group of fishes, the salmonids, from the Pacific coastal waters of North America and to describe the successful experimental transmission of the condition.

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Materials and methods — Observations on natural EN — These were made on chum (*Oncorhynchus keta*) and pink

(*O. gorbuscha*) salmon reared in seawater pens in Departure Bay, B.C.

Experimental transmission of EN — Fish used in these experiments came from lots that had been examined and found to be EN-free. Diagnosis of EN was based on an examination of Giemsa-stained blood films. A fish was diagnosed as EN-positive if any inclusion-bearing erythrocytes were detected in the first 50 microscopic fields examined (100× objective lens); if inclusion-bearing erythrocytes were not found, it was considered as EN-free. Three experiments were conducted.

The first experiment was to determine whether the EN agent was filterable and infectious. Inocula were, therefore, aseptically passed through 0.45-μm membranes and then serially passaged in fish. Three serial passages were made in chum salmon and a fourth in pink salmon. Ten control and 10 test fish were used for each passage; they were kept in separate seawater tanks in which temperatures ranged from 8 to 12°C over the course of the experiment. Control chum salmon received a single intraperitoneal (i.p.) inoculation (0.5 mL/100–200-g fish) of sterile Hanks' balanced salt solution (HBSS) and the test fish a filtered tissue extract. Pink salmon were smaller; they received 0.1 mL/10 g-fish. The tissue extract was prepared by homogenizing infected chum salmon kidney and spleen in 19 vol of cold HBSS, centrifuging at 500 × *g* for 30 min, and aseptically passing the supernatant through a 0.45-μm membrane filter. The fish were examined for signs of EN at 2 or 3 wk post-inoculation (P.I.).

In the second experiment 24-g chinook (*O. tshawytscha*) and 10-g coho (*O. kisutch*) and sockeye (*O. nerka*) salmon from freshwater were tested for susceptibility to EN. Fish received 0.1 mL i.p. of infected chum salmon tissue filtrate (the same filtrate used to inoculate the pink salmon in the first experiment) or sterile HBSS. Young pink salmon were included as known susceptibles. Test and control fish (10 of each) were then held separately in 10°C seawater (pink salmon), in 14°C freshwater (chinook and coho salmon), or where enough fish were available in both (sockeye salmon). Fish were examined for signs of EN 3 wk later.

In the third experiment the course and lethality of the infection were investigated in 100-g chum salmon. Fish were inoculated with 0.5 mL i.p. of infected chum salmon tissue filtrate or with the heated filtrate (60°C for 15 min). The two groups of fish (10 fish in each) were then held separately in seawater at 10–12°C. Blood from these fish was examined for signs of EN at 12, 48, and 202 d P.I.

Transmission electron microscopy — Blood samples were fixed for 10 min in 100 vol of cold 4% glutaraldehyde maintained at pH 7.3 with 0.1 M phosphate buffer. The blood cells were then washed 3 times in the cold buffer, postfixed for 2 h in cold Millonig's buffered osmium tetroxide, dehydrated in a graded ethanol series, taken into propylene oxide, and embedded in Epon 812. Thin sections, stained with 1% (wt/vol) uranyl acetate and Reynolds' lead citrate, were then examined for the virus.

Results and Discussion — Natural EN in Pacific salmon: history and clinical picture — Erythrocytic necrosis was first observed in 1964 among locally propagated chum salmon. It was next recognized in 1972 in cultured pink salmon and since then has been encountered frequently in chum and pink salmon held in net pens. Chinook, coho, and sockeye salmon reared in nearby pens never appeared to acquire the disease.

To date, EN has only been diagnosed in salmon reared in seawater, thereby suggesting that the causal agent might be of marine origin. Infections were diagnosed over a wide range of temperatures (6.5–19°C), but seemed to be most severe during the summer. Affected fish were usually at least 12 mo old, but severe infections have been observed in 8-mo-old chum and 6-mo-old pink salmon.

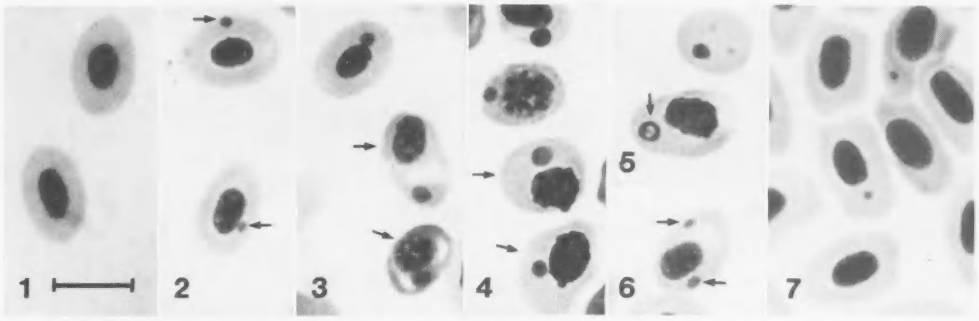
The disease appeared to be chronic and at times over 80% of a given lot showed infection. Mortality rates due to EN alone appeared to be low (up to 0.3%/d), but natural outbreaks were usually complicated by vibriosis or bacterial kidney disease (BKD).

In fish dying of uncomplicated EN, the internal organs such as kidney and spleen were usually bacteria-free. However, filtrates of these organs were infectious (see next section). The filtrates contained a virus, but attempts to isolate the virus in established cell lines such as rainbow trout gonad, chinook salmon embryo, and fathead minnow cells cultured at 8 and 15°C for 3 wk were unsuccessful.

Gross and histological signs of EN were neither striking nor pathognomonic, and the disease might easily have gone undiagnosed had Giemsa-stained blood films not been examined. Grossly, fish with advanced EN were anemic. The anemia was usually evident in the pale gills, heart, liver, kidney, and alimentary tract. Also, hematocrits of only 2–10% were very common and the blood clotted slowly or not at all. Histologically, the only noteworthy changes were in the kidney, which showed extremely active hematopoiesis.

An examination of Giemsa-stained blood films revealed that only the erythrocytes were affected. Unlike normal erythrocytes (Fig. 1), affected cells usually contained a rounded, pink- or magenta-staining, cytoplasmic inclusion body, 0.8–4.0 μm in diameter. In advanced infections, virtually all of the erythrocytes were affected, and many of them showed degenerative changes. The blood picture (Fig. 2–7) was strikingly similar to that observed for virus-associated EN in other fishes (Johnston and Davies 1973; Appy et al. 1976; Sherburne 1973; Reno et al. 1978), reptiles (Stehbens and Johnston 1966), and amphibians (Bernard et al. 1968).

Experimental transmission — Transmission trials clearly showed that EN was infectious and that the agent was filterable. Nine of 10 pink salmon inoculated with fourth passage material (equivalent to 2×10^{-11} dilution of the original material) showed EN at 3 wk. Controls remained EN-free. Furthermore, electron microscopy showed viral particles (virions) in chum salmon with EN and they were similar in size and morphology (Fig. 8, 9) to those observed in pink salmon with EN. It seems inescapable, therefore, that virus is responsible for the disease in chum and pink salmon.



FIGURES 1–7. Light micrographs illustrating viral erythrocytic necrosis in chum (*Oncorhynchus keta*) and pink (*O. gorbuscha*) salmon. Giemsa-stained erythrocytes. Bar scale = 10 μm.

FIG. 1. Uninfected, mature erythrocytes (healthy chum salmon): the elliptical erythrocytes possess a central, elliptical nucleus and lack cytoplasmic inclusions. FIG. 2. Infected erythrocytes (chum salmon): each erythrocyte (typically) contains a single, rounded, uniformly stained, inclusion body (arrows), the location of which in the cytoplasm may vary. FIG. 3. Three inclusion-bearing erythrocytes (chum salmon), two of which (arrows) show clear signs of degeneration: irregular outlines, nuclear displacement, and cytoplasmic vacuolation. FIG. 4. Inclusion-bearing erythrocytes (chum salmon) two of which (arrows) show degenerative signs including condensation and possibly leakage of nuclear material. FIG. 5. Two infected erythrocytes (chum salmon): the upper one appears to be enucleated; the lower one contains a peripherally stained inclusion (arrow). FIG. 6. An infected, degenerating, and rarely seen erythrocyte (chum salmon) containing two inclusions (arrows). FIG. 7. Normal and inclusion-bearing erythrocytes from a lightly infected pink salmon.

The virus displayed a surprising degree of host specificity. The same chum salmon filtrate that induced EN in 9 of 10 pink salmon in 3 wk failed to infect chinook, coho, and sockeye salmon. These results confirmed field observations which suggested that chinook, coho, and sockeye salmon were resistant to EN.

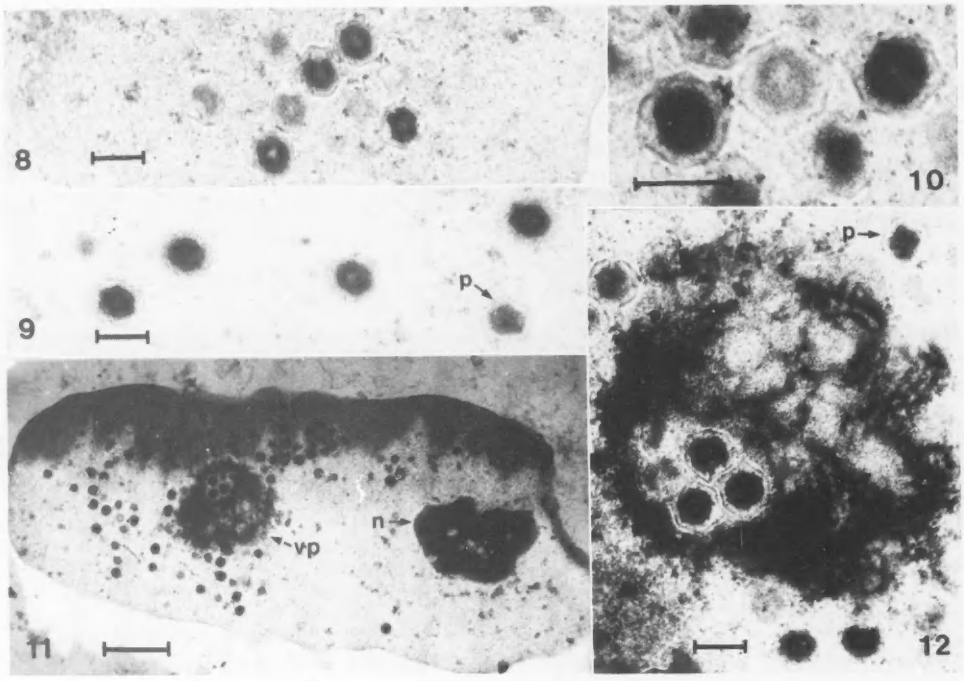
Under our experimental conditions, induced EN was slow to develop; it did not appear to be particularly lethal and some fish even appeared to recover from it. In chum salmon challenged with an infected chum salmon tissue filtrate, the proportion of EN-infected fish increased from 50% at 12 d P.I. to 100% (10/10 fish) at 48 d P.I. By 48 d P.I., anemia, characteristic of the natural disease, had also developed. At 48 d P.I. hematocrits for test and control fish averaged 29% (range for 10 fish, 26–31%) and 45% (range for nine fish[1], 41–51%), respectively. Seven of the test fish escaped a natural infection with BKD and survived to 202 d P.I.; of these, four had apparently become EN-free. Control fish in this experiment had been injected with the heated (60°C for 15 min) infected chum tissue filtrate instead of sterile HBSS; these fish did not develop EN, indicating that the EN virus was labile to mild heating.

Electron microscopy — Virions, described below, were never observed in the erythrocytes of healthy fish; they were seen only in the erythrocytes of chum and pink salmon that had been diagnosed as having EN by light microscopy. They were always located in the cytoplasm and were the only recognizable foreign entities present. When filtered tissue extracts from EN-infected chum salmon were injected into healthy chum salmon, virions similar to those found in the donor fish appeared in the erythrocytes of the recipient fish. The occurrence of the virus coincided with that of intraerythrocytic inclusions typical of EN. These observations further strongly support the hypothesis that the virions are responsible for EN.

The virions were icosahedral (see Stoltz 1971) because sections through them exhibited hexagonal and pentagonal profiles (Fig. 9, 12). Measurements between opposing apices of the hexagonals averaged 190 nm (range for 30 virions, 179–199 nm). The virions (Fig. 10) possessed an electron-dense coat, about 8 nm thick, a central circular-to-hexagonal 130-nm nucleoid, and a 22-nm intervening electron-translucent zone. Some nucleoids stained uniformly, while others had a small, central electron-translucent zone. The particle size is smaller than that reported for virions in the blenny (200–300 nm) and cod (310–360 nm), but larger than that reported by Reno et al. (1978) for virions in the Atlantic herring (146 nm).

Inclusions, evident in Giemsa-stained blood films, probably represented virion aggregates (Fig. 8) and viroplasm (viral precursor material) (Fig. 11, 12) because electron microscopy did not reveal any other structures that might account for the inclusions. The inclusions were feebly Feulgen-positive, but were not stained by the periodic acid-Schiff (PAS) method. These results indicated that the inclusions contained deoxyribonucleic acid (DNA) rather than ribonucleic acid and suggest that the virus was of the DNA type.

[1]Ten control fish were injected, but one of them died of unknown causes within 24 h of injection.



FIGURES 8–12. Electron micrographs of viral erythrocytic necrosis in chum (*Oncorhynchus keta*) and pink (*O. gorbuscha*) salmon.

FIG. 8. A loose aggregate of hexagonal virions in a chum salmon erythrocyte. Bar scale = 200 nm. FIG. 9. Virions in a pink salmon erythrocyte showing hexagonal and pentagonal (p) profiles. Bar scale = 200 nm. FIG. 10. Virions in a chum salmon erythrocyte showing their structure and their different nucleoid staining reactions. Bar scale = 200 nm. FIG. 11. A chum salmon erythrocyte containing many cytoplasmic virions; the dark area (n) at the right is believed to represent the remains of the cell's nucleus, while that at the left (vp) is believed to represent viroplasm. Bar scale = 1 μm. FIG. 12. Enlargement of electron-dense material, labeled vp in Fig. 11, which is believed to represent viroplasm. The viroplasm differs from nuclear material in being coarsely cord-like, in lacking a limiting membrane, and in containing virions. Hexagonal and pentagonal (p) virion profiles are evident. Bar scale = 200 nm.

General remarks — The present findings clearly indicate that EN in salmon is due to a virus, very likely an ICDV. We propose, therefore, that the disease be termed viral erythrocytic necrosis or VEN. The term is more descriptive of the condition than PEN, and it could also be used more widely to designate the disease in other fish and animals. Furthermore, when applied to fish, it avoids the redundancy in phrases such as "piscine erythrocytic necrosis in salmon" that would otherwise be inevitable.

Viral erythrocytic necrosis promises to be a problem in the mariculture of chum and pink salmon, and much remains to be learned about the disease. The responsible virus has yet to be isolated, conditions predisposing to the disease have yet to be determined, and the source of the virus remains to be identified. With regard to the last point, many species of marine fish apparently have the disease (Walker and Sherburne 1977), and certain of them may serve to infect salmon and perhaps other anadromous fishes (see Sherburne 1977). We have preliminary evidence to indicate that Pacific herring, *Clupea harengus pallasi*, also suffer from VEN, and that tissue filtrates from infected herring induce the disease in chum and pink salmon. Unfortunately, until the causal virus(es) can be isolated, knowledge about VEN will be slow in accumulating.

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Leaping Behavior of Juvenile Coho (*Oncorhynchus kisutch*) and Atlantic Salmon (*Salmo salar*)

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Juveniles of coho (*Oncorhynchus kisutch*) and Atlantic salmon (*Salmo salar*) proved capable of leaping falls at least 5 body lengths in height. No species differences were apparent: both species leapt lower falls (12 cm) more readily than higher ones (27 and 57 cm) and proportionately more leaps occurred on days with temperatures between 14.0 and 17.0°C than on days with lower temperatures.

Key words: fish, freshwater fish, behavior, migrations, environmental conditions, temperature effects

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Les saumoneaux, tant coho (*Oncorhynchus kisutch*) qu'atlantiques (*Salmo salar*), se sont montrés capables de sauter des chutes d'une hauteur d'au moins 5 fois la longueur de leur corps. Il n'y a pas de différences spécifiques apparentes : l'une et l'autre espèce sautent de basses chutes (12 cm) plus volontiers que des chutes plus hautes (27 et 57 cm). Le nombre de sauts est proportionnellement plus élevé pendant les jours où la température se situe entre 14.0 et 17.0°C que pendant les jours où les températures sont plus basses.

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LEAPING behavior of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) was described by Stuart (1962). He found that in a pool where scouring and depositional processes were in equilibrium, a standing wave formed at the foot of the falls which stimulated and to some extent oriented the leap. For a falls to be easily surmountable, the water should enter the chute from a pool of low velocity and turbulence, and tumble nearly vertically into the falls pool below. From observations at natural falls, Stuart concluded that Atlantic

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salmon and brown trout can leap a height of 10 body lengths under optimum conditions.

Little other experimental work appears to be reported on the leaping behavior of fishes. This is unfortunate since knowledge of the leaping of different fish species might provide the performance criteria for construction of specialized obstructions (e.g. weirs) or passes (e.g. fish ladders) designed to segregate species ascending a stream, as suggested by Mason and Machidori (1976). This note provides some limited experimental data on leaping behavior of juvenile coho (*Oncorhynchus kisutch*) and Atlantic salmon for falls of different heights and temperatures.

Materials and methods — The experiment was conducted in a laboratory flume consisting of four compartments: a header tank, from which water flowed to a header pool, then into a falls pool, and finally into a collection tank where it was pumped back to the header tank. Fish were restricted by nets to the header and falls pools.

The header pool was 100 × 53 × 33 cm. The water fell from this pool through a trapezoidal notch 20 cm wide at the bottom. The water at the lip of the falls was about 10 cm deep. A submerged net across the mouth of the falls was attached to a screen which projected 10 cm back into the header pool 1–2 cm below the surface, so that fish could not be swept down the falls once they had jumped to the header pool.

The falls pool was 167 × 100 cm. Height of the falls was controlled by raising or lowering the water level in the falls pool through the addition or removal of stop logs separating the falls pool from the collection tank. Because the water head between the collection and header tanks was constant regardless of the depth of the falls pool, the volume of water passing over the falls was constant at all fall heights. Fall height could be varied from 0 to 57 cm, with a minimum depth in the falls pool of 110 cm at maximum fall height. Stuart (1962) stated that pool depth should equal or exceed 1.25 times fall height to meet optimal hydraulic conditions for leaping.

A small amount of water continually flowed into the apparatus to replace that lost by leakage and to maintain ambient temperatures between 6 and 17°C. Temperature was recorded daily, except on 11 d (7% of total), during the experiment and it frequently varied by 1–2°C on successive days. Ambient lighting from the laboratory windows was supplemented during working hours by a 200-W incandescent bulb suspended 3 m above the flume.

Seventeen underyearling coho and a similar number of yearling Atlantic salmon were collected in October from "Frost Fish Creek" near St. Andrews, N.B. Both species were from natural spawning, the coho deriving apparently from stock that was released or had escaped from fish culture operations in the United States (Symons and Martin 1978). Each species was held in a separate tank in the laboratory at water temperatures similar to those in the falls flume. A daily photoperiod of 12 h light was provided over the holding tanks until December 28, after which daily light was extended by 15 min each week until the experiment terminated March 28. Fish were fed sparingly on mealworms (*Tenebrio* sp.). Coho used in experiments ranged from 7.1 to 11.5 cm; Atlantic salmon from 7.5 to 12.0 cm, fork lengths.

The experimental method consisted of placing five individuals of one species in the falls pool of the flume and recording the number in the header pool once or twice daily for the following 3–4 d. Fish were measured (fork length) before being placed in the flume, and those found in the header pool were removed, measured, and returned to the appropriate holding tank. The species to be tested was chosen at random with the restriction that the number of tests on each species was kept approximately equal throughout the duration of the exeriment. Because the stock of fish was small, individuals had to be reused in later tests, but by cold-branding fish as they were returned to the holding tanks the rotation and use of all healthy individuals were assured.

Three fall heights, 12, 27, and 57 cm, measured from surface of the falls pool to surface of the header pool, were used. The height of falls for each 3–4 d test was also chosen at random, again with the restriction that the number of tests at each height was kept approximately equal. The experimental period ran from November 18 to March 28.

TABLE 1. Comparison of number of test-fish days (= number of observation days × number of fish in falls pool within the previous 24 h) at three fall heights and seven temperature classes, and the number of fish leaping at each condition (in parentheses).

	Temperature (°C)							Totals at each fall ht
	Not recorded	<8.0	8.0–9.9	10.0–11.9	12.0–13.9	14.0–15.9	16.0–17.0	
				Coho salmon				
Fall ht (cm)								
12	0	0	1 (0)	28 (3)	17 (2)	14 (1)	3 (2)	63 (8)
27	5 (0)	4 (0)	13 (1)	34 (2)	51 (2)	0	0	107 (5)
57	25 (0)	0	5 (0)	23 (0)	40 (0)	10 (2)	0	103 (2)
Totals at each temp	30 (0)	4 (0)	19 (1)	85 (5)	108 (4)	24 (3)	3 (2)	273 (15)
				Atlantic salmon				
Fall ht (cm)								
12	14 (1)	0	4 (1)	25 (4)	21 (2)	6 (3)	0	70 (11)
27	35 (0)	5 (0)	0	20 (0)	25 (0)	20 (0)	0	105 (0)
57	10 (0)	0	10 (0)	0	59 (0)	5 (0)	5 (1)	89 (1)
Totals at each temp	59 (1)	5 (0)	14 (1)	45 (4)	105 (2)	31 (3)	5 (1)	264 (12)

TABLE 2. Numbers (percentage in parentheses) of tested fish that leapt into the header pool or remained in the falls pool at three fall heights.

Fall ht (cm)	Not leaping	Leaping
	Coho salmon	
12	17	8 (32)
27	25	5 (17)
57	28	2 (7)
	Atlantic salmon	
12	19	11 (37)
27	30	0 (0)
57	24	1 (4)

Results — There was no observable seasonal trend in experimental temperature, nor was there any obvious seasonal effects on frequency of leaping. The observations on leaping behavior were therefore categorized according to the height and temperature of the falls (Table 1) without regard to season.

More fish of both species leapt the low falls (12 cm) than leapt the intermediate (27 cm) or high (57 cm) falls (Table 1), but these data were not amenable to statistical testing. Therefore the numbers of fish in each test that leapt or did not leap were summed for each fall height (Table 2). A statistically higher proportion of Atlantic salmon leapt the 12-cm falls than leapt the 27- and 57-cm falls combined ($P < 0.001$, chi-square test). The results for coho were not significant ($P < 0.1$). One Atlantic salmon and two coho leapt the highest falls, this being a leap of 5.2 body lengths for the Atlantic salmon, and 5.4 and 5.7 body lengths for the coho.

Effects of temperature on leaping behavior could not be tested statistically, but both species performed proportionately more leaps per test-fish day ($\geq 10\%$, all fall heights combined) at temperatures above 14.0°C than at lower temperatures ($<9\%$). The two coho leaping 57 cm did so at a temperature of 14.5°C, and the Atlantic salmon leaping this height did so on the day with the highest recorded test temperature (16°C) for this species (Table 1)

The proportion of fish that leapt from falls to header pool on the 3 or 4 successive d of each test varied between 1 and 6%, with no consistent trend over the length of the test. There were no consistent or statistically significant species differences in leaping behavior.

Discussion — Huntsman (1945) and Stuart (1962) described upstream movements of juvenile Atlantic salmon as occurring in spring. These movements became sporadic by mid-June (Stuart 1962) and were reversed in the fall. The present experiment was performed from midwinter through early spring, the fish being held under conditions of increasing photoperiod. No seasonal changes in leaping behavior were detected. However, temperature, though not controlled experimentally, did appear to influence leaping because proportionately more leaps occurred between 14 and 17°C than at lower temperatures. Peterson (1973) found that the preferred temperature of juvenile Atlantic salmon ranged between 14.6 and 17.5°C, and Fisher and Elson (1950) showed that the dart-forward response to an electrical shock reached a maximum within this range of temperatures. That maximal frequency and heights of leaping should also occur near the preferred temperatures seems reasonable, but needs confirming.

Huntsman (1945) noted that Atlantic salmon fry were stopped in their upstream movement by falls from culverts of ~ 30 cm, and yearlings were stopped by falls of ~ 45 cm. The present results suggest that falls of these heights should not have arrested the upstream movements of these fish if the optimum hydrodynamic conditions specified by Stuart (1962) were in force. The limiting feature of culverts, assuming they were in place for sufficient time for scouring and deposition in the pool to have reached equilibrium, would appear to be the lack of a header pool with low velocity and turbulence.

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Modified Staaland Device with Automatic Recording Techniques for Determining Salinity Preference in Fishes

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Modifications were made in the design and filling procedure of the Staaland device used to study salinity preference in fish. Two photographic recording techniques that eliminate the need for direct observation of fish activity and allow for continuous monitoring of fish movement throughout several daily photoperiodic cycles are described.

Key words: salinity, preference, gradient, fish, photography, recording

FIVIZZANI, A. J., AND R. E. SPIELER. 1978. Modified Staaland device with automatic recording techniques for determining salinity preference in fishes. J. Fish. Res. Board Can. 35: 910–912.

Les auteurs ont modifié le modèle et le procédé de remplissage de l'appareil de Staaland servant à déterminer les préférences de salinité chez les poissons. Ils décrivent deux méthodes photographiques d'enregistrement qui éliminent le besoin d'observer directement l'activité des poissons et permettent un contrôle continu des mouvements des poissons durant plusieurs cycles photopériodiques quotidiens.

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VARIOUS devices have been employed to study developmental or physiological alterations in teleost salinity preference. Early investigations utilized partitioned chambers in which fish selected between only two different salinities (Baggerman 1957, 1963; Houston 1957; McInerney 1964). The use of other devices that allow for a greater range of salinity choices have inherent disadvantages. Salinity preferences of invertebrates have been studied using gradients of more than two salinities which were separated by density layering in vertical or slanted chambers (Aldrich 1963; Keiser and Aldrich 1973). A multiple salinity vertical chamber has also been used to test salinity preference of young salmon (Hurley and Woodall 1968) and two species of *Fundulus* (Fritz and Garside 1974). However, methodologies based upon vertical layering introduce a gradient of hydrostatic pressure as well as salinity. The use of continuous flow salinity gradients (i.e. Höglund 1951; Creutzberg 1961; Otto and McInerney 1970; and Hansen 1972) provides an adequate choice of salinities but economically their use is most feasible in localities with an abundant supply of seawater. In addition, the use of a continuous flow gradient may elicit rheotactic responses from the experimental animal.

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Staaland (1969) introduced a static salinity gradient to study salinity preference in invertebrates. The Staaland device is a partitioned aquarium with a horizontal series of graded salinities (Fig. 1). The graded salinities are separated by discontinuity layers or interfaces formed as a result of differential density layering. There is an abrupt change in salinity at each transition layer. Experimental animals are thus given a series of discrete choices among a gradation of salinities (i.e. 0, 7, 14, 21, 28, 35‰) with a distinct option between pairs of salinities at each interface.

The Staaland device was recently utilized to study salinity preference of larval and juvenile grunion by Reynolds and Thomson (1974). We have modified the design of the original Staaland device and simplified the procedure of filling the device to study salinity preference of *Fundulus grandis* (Spieler et al. 1976; Fivizzani 1977). Previous studies on fish salinity preference apparently have all relied upon direct observation. We have utilized two photographic recording techniques to continuously monitor the location of fish in a salinity gradient for extended periods of time (several days). These methods allow for a more detailed quantitative analysis of fish behavior without any interaction between the subject and the observer.

Modified Staaland device — The original gradient

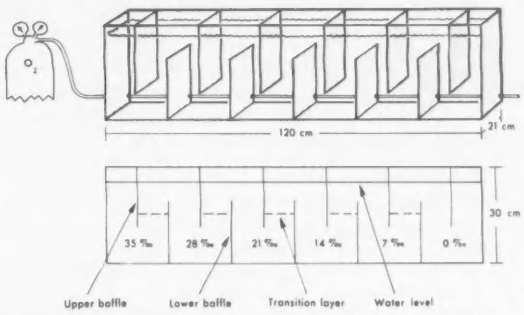

FIG. 1. Modified Staaland salinity gradient device for testing salinity preference of small fish. Upper diagram is a top view of the chamber and the lower diagram illustrates a schematic frontal view of the chamber.

chamber of Staaland (1969) was constructed of clear plexiglass only. However, in our preliminary studies the fish required approximately 30 min to learn to negotiate the barrier baffles of a gradient device constructed of clear plexiglass. For this reason, we constructed the end pieces and baffles of our gradient system from black plexiglass; the front, back, and bottom pieces were made of clear plexiglass. The use of black baffles eliminated much of the trial and error behavior noted in the clear plexiglass device and therefore reduced the time required for a naive fish to learn to negotiate the chamber. The thickness of the baffles was 3.18 mm and that of all other plexiglass components was 4.76 mm. A silastic medical grade tubing (3.35 mm ID × 4.65 mm OD: Dow Corning, 601-335) with a high oxygen permeability was inserted along the back wall through holes in the lower baffles located 3 cm above the tank bottom. Oxygen permeability of silastic is 4–24 times greater than through rubber tubing which was utilized in the original Staaland device (Lebovits 1966). Initially only one end of the tubing was connected to an oxygen tank through a regulator to deliver a continuous 55.2 kPa. This system maintained dissolved oxygen levels within 2‰ of saturation in all compartments over a 4-d period during which a large *Fundulus grandis* (approximately 10 cm) was tested. In later experiments both ends of the tubing were connected to the regulator to equalize the pressure throughout the tube.

Modifications were also made in the method of filling the apparatus. We believe that our filling procedure reduces the effort required to establish the gradient of salinities and allows for simplification of the design of the chamber by eliminating the necessity for a watertight chamber top and filling holes. In our procedure the salinity gradient is established by initially filling each of the lower compartments with waters of its respective salinity up to the top edge of the lower baffles. The waters are siphoned through large diameter tubing from overhead 20-L reservoirs. All subsequent additions to the apparatus are accomplished by means of gentle gravity flow from the overhead reservoirs through small diameter (4 mm) plastic tubing into the appropriate compartment. The flow rates through the tubing are regulated by plastic needle valves which are inserted in the tubing. After the initial filling of the lower compartments, water of the lowest salinity only is added slowly (approximately 125 mL/min) to the first compartment (0‰) which causes the contents of this compartment to flow over into the second compartment. The overflow from one compartment into adjacent compartments of higher salinities continues in series from the first to the last compartment. The transition layer formed between two adjacent salinities is visually apparent due to differences in the refractive index at the interface. Gentle flow rates are required to minimize turbulence and allow for the formation of discrete transition layers. As the transition layer between two salinities approaches the appropriate location (see Fig. 1) the flow of water into the higher salinity compartment is initiated and adjusted to stabilize the interface location.

The gradient is filled to a level sufficient for the fish to swim over the lower baffle (approximately 6 cm over the top of the lower baffle) for tests of small fish (e.g. *Fundulus grandis*). Although the movement of the fish through the gradient temporarily disturbs the transition layers, they are quickly reestablished. Some mixing does occur, however, and when the salinity in any compartment differs by more than 2‰ from the original salinity, the entire apparatus is drained and a new gradient is established. The gradient can normally be used continuously for 2–4 d of testing. The most drastic disturbance to the gradient results from the retrieval of fish from the device.

Two automatic photographic methods can be used to eliminate the need for direct observation. The first photographic method allows for recording the activity of fish continuously for several days. During this time the fish continues to be subjected to the acclimation photoperiodic regime with the exception that dim light (<2 lx) is substituted for total darkness. In one study (Spieler et al. 1976), photographs of the position of the fish in the salinity gradient were taken every 30 min throughout the day with a Nikon F camera using a motor drive and interval timer. In addition to the salinity gradient, a digital clock is included in the camera field of view to allow for rapid correlation of the location of the fish in the gradient and the time of day. Construction paper is attached to wooden framework from the camera to the sides of the gradient. This allows the camera to be approached without disturbing the fish. Pictures are taken on Tri-X (Kodak) film at an ASA of 3200 (f 5.6, shutter speeds $\frac{1}{250}$ s and 1 s; light and "dark" periods, respectively). Camera settings must be changed twice a day, at the beginning of the light portion of the photoperiod and again at the beginning of the dark portion. The film clearly shows the position of the fish during the day and night when projected with a filmstrip viewer.

To obtain a more detailed analysis of the movements of fish that are not subjected to a light–dark cycle, an alternate recording method, which uses a Minolta XL-

400 movie camera, can be employed. This camera is equipped with a built-in "intervalometer" which allows for single frame exposure frequencies from 18 frames/s to 1 frame/min. The cost of this camera is considerably less than the total cost of the 35-mm camera, motor drive, and interval timer which are required for the previously described photographic method. The use of Kodak Ektachrome 160 Type A film permits photography under normal room lighting intensity (approximately 500 lx). The location of the fish is easily observable when individual frames are viewed through a binocular dissection microscope.

We believe that the utilization of the modified Staaland salinity gradient device, in conjunction with either of the photographic procedures, may be of benefit to those individuals who are interested in observing salinity preferences of fish. This system may be utilized to monitor fish preferences continuously for several days during an uninterrupted daily photoregime, or may be utilized to study in more precise temporal detail the preference pattern of fish under normal laboratory illumination.

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Calculation of the Average Age of Sexual Maturity in Marine Mammals

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DEMASTER, D. P. 1978. Calculation of the average age of sexual maturity in marine mammals. J. Fish. Res. Board Can. 35: 912–915.

The average age of sexual maturity and first pregnancy are important criteria in evaluating the status of a population. However, the estimation procedure for these statistics should be sensitive to the different distributions of age-specific reproductive data and should also incor-

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porate a variance estimate to facilitate comparisons between populations. The described procedure lends itself well to age-specific data and should be useful in discerning differences between populations of ½-yr or more, if a sample of at least 25 is available for each age-class.

Key words: reproduction, marine mammals, sexual maturity

DeMaster, D. P. 1978. Calculation of the average age of sexual maturity in marine mammals. J. Fish. Res. Board Can. 35: 912–915.

Dans l'évaluation de l'état d'une population, l'âge moyen de la maturité sexuelle et la première grossesse sont des critères importants. Cependant, la méthode d'estimation de ces statistiques devrait être assez sensible aux différentes distributions de données sur la reproduction spécifiques à l'âge et devrait également inclure une estimation de la variance, afin de faciliter les comparaisons entre populations. La méthode que nous décrivons ici se prête bien aux données spécifiques à l'âge et devrait permettre de déceler des différences de ½ a ou plus entre populations, si on a un échantillon d'au moins 25 individus de chaque classe d'âge.

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The age of sexual maturity has been described as an important criterion for evaluating the status of a population (Eberhardt and Siniff 1977). However, individual variations in the exact age at which a female first ovulates or the age at which a male initiates sperm production makes this statistic difficult to use. Sergeant (1966) presents comparative harp seal data and suggests that exploitation has significantly reduced the average age of sexual maturity in females. His method of determining this average involves taking the median of those ages in which ovulation rates were >0, but less than unity. This has the disadvantage of weighting all age-classes equally, even if the age-specific ovulation rates are drastically different.

A second technique to determine the average age of sexual maturity involves plotting percent sexually mature versus age, and interpolating the graph for the age associated with 50% sexual maturity. This method has the disadvantage of producing estimates that are not associated with confidence intervals, and therefore, does not lend itself to a statistical analysis of differences in the mean age of sexual maturity between two populations.

Laws et al. (1975) present a technique to calculate the average age of sexual maturity for animals that have an extended breeding season. However, for those species with a discrete breeding season, the following procedure seems more appropriate in estimating the average age of sexual maturity.

The estimate of the average age of sexual maturity in females is as follows:

$$f(x) = \frac{t(x)}{n(x)}, \tag{1}$$

where x = age of female, $f(x)$ = estimated probability of ovulating at or before age x, $t(x)$ = number of females in sample of age x who have ovulated, and $n(x)$ = number of females of age x in sample. With this definition of $f(x)$, the estimated probability of first ovulating at age x is

$$P(x) = f(x) - f(x-1), \tag{2}$$

where $P(x)$ = estimated probability of first ovulating at age x, and comes from the relationship

$$f(x-1) + P(x) = f(x). \tag{3}$$

The average age of sexual maturity is then calculated as

$$\bar{x} = \sum_{x=0}^{w} (x)P(x), \tag{4}$$

where $\bar{x}$ = average age of sexual maturity and w = maximum age in sample. The estimated variance for $\bar{x}$ is

$$v(\bar{x}) = \sum_{x=0}^{w-1} \frac{f(x)(1-f(x))}{n_x - 1} + \frac{w^2 f(w)(1-f(w))}{n(w)-1}. \tag{5}$$

The main assumption associated with this estimate is that all of the $f(x)$'s are independent of each other. In most samples, where individuals are collected and not returned to the population, this assumption is met. Given that $\bar{x}$ is at least 1, and the sampled population is representative of the entire population, a 95% confidence interval can be approximated by

$$95\%\ \text{CI} = \bar{x} \pm 1.96(v(\bar{x}))^{\frac{1}{2}}. \tag{6}$$

Table 1 (hypothetical data) presents this procedure as it is used in estimating the average age of sexual maturity, as well as the variance associated with this average. Comparisons with other populations could be made with a modified t-test (Snedecor and Cochran 1967, p. 114), with $\sum_{x=0}^{w} n_x$ as the sample size for a particular sample. Because of sampling error, some values of $P(x)$ may be negative. Equation (4) may still be used in this case, but a more satisfactory alternative may be to obtain $f(x)$ values from a curve fitted to a plot of $f(x)$ versus x. With these fitted values of $f(x)$, a new set of $P(x)$ values can be calculated (Laws et al. 1975).

Equation (5) shows that as the sample size for each indeterminate age-class (i.e. years where $0 < f(x) < 1$) increases, the variance of $\bar{x}$ is reduced. A reasonable estimate of the sample size necessary to detect ½-yr differences in $\bar{x}$ between two populations can be derived as follows.

If sample sizes are constant in each age-class and $f(w) = 1$, then the true variance of $\bar{x}$ is

$$V(\bar{x}) = \sum_{0}^{w-1} \frac{f(x)(1-f(x))}{n}. \tag{7}$$

If there are 3 indeterminate yr, a maximum variance estimate would be

$$V(\bar{x})_{\max} = \frac{(0.5)(0.5) + (0.5)(0.5) + (0.5)(0.5)}{n} = \frac{0.75}{n}. \tag{8}$$

TABLE 1. Calculation of average age of sexual maturity in a hypothetical population of females. Average age of sexual maturity = 4.40, var(x) = 0.032.

Age (x)	Number of females observed $n(x)$	Number ovulated $t(x)$	P (1st ovulation at or before age x) $f(x)$	P (1st ovulation at age x) $P(x)$	$xP(x)$
0	35	0	0.0	0.0	0.00
1	30	0	0.0	0.0	0.00
2	25	0	0.0	0.0	0.00
3	20	4	0.2	0.2	0.60
4	20	12	0.6	0.4	1.60
5	15	12	0.8	0.2	1.00
6	15	15	1.0	0.2	1.20
7	10	10	1.0	0.0	0.00
8	10	10	1.0	0.0	0.00
					4.40

TABLE 2. Calculation of average age of first pregnancy in a hypothetical population of females. Average age of first pregnancy = 3.34, var(x) = 1.21, a = 4.

Age (x)	Number of females observed $n(x)$	Number of pregnant females $y(x)$	P (pregnant at or before age x) $z(x)$	P (1st pregnant at age x) $r(x)$	$xr(x)$
0	35	0	0.00	0.0	0.00
1	30	0	0.00	0.0	0.00
2	25	6	0.24	0.24	0.48
3	20	13	0.65	0.41	1.23
4	20	16	0.80	0.15	0.60
5	15	12	0.80	0.16	0.80
6	15	12	0.80	0.032	0.19
7	10	8	0.80	0.0064	0.04
8	10	8	0.80	0.000128	—
					3.34

The formula that relates sample size to significant differences is

$$\frac{\bar{x}_1 - \bar{x}_2}{\sqrt{V(\bar{x}_1) + V(\bar{x}_2)}} = t_{0.05,\mathrm{df}}, \tag{9}$$

which assumes $V(\bar{x}_1) \cong V(\bar{x}_2)$.

If $\bar{x}_1 - \bar{x}_2$ is set equal to 0.5, and $t_{0.05}$, df = 2, then

$$\frac{0.5}{\sqrt{\frac{0.75}{n} + \frac{0.75}{n}}} = 2, \tag{10}$$

or

$$n = \frac{(1.5)(4)}{0.25} = 24.$$

Therefore, if differences of at least ½-yr are to be determined significant, a reasonable sample size for each indeterminate age-class in each population may be ~25.

In addition to estimating the average age of sexual maturity, this procedure can be used to estimate the average age of first pregnancy. However, because the probability of a female being pregnant may never reach unity, there exists a positive probability that at age x a female will reproduce for the first time, even if the difference between the probability of being pregnant for two consecutive age-classes is 0. Therefore, the estimate of the average age of first pregnancy is

$$z(x) = \frac{y(x)}{n(x)}, \tag{11}$$

where $z(x)$ = estimated probability of being pregnant at age x, $y(x)$ = number of females pregnant at age x in sample, and $n(x)$ = number of females in sample. For $x \leq a$, where a equals the age at which $z(x)$ reaches its maximum,

$$r(x) = z(x) - z(x-1), \tag{12}$$

where $r(x)$ = {estimated probability that a female is first pregnant at age x}, and for $x > a$,

$$r(x) = z(a)(1 - z(x))^{x-a}. \tag{13}$$

The average age of first pregnancy and the associated variance are calculated as before, except that $r(x)$ replaces $P(x)$, and $z(x)$ replaces $f(x)$. Table 2 illustrates with hypothetical data the way in which this procedure should be used.

The estimation of the average age of sexual maturity

or age of first pregnancy should prove useful in evaluating population trends or comparisons. The described procedure should provide estimates of both the mean age and its variance. With age-specific sample sizes >25, the differences of $\frac{1}{2}$-yr or more should be significant.

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PERSPECTIVES

Federal–Provincial Strategic Planning for Ontario Fisheries: Management Strategy for the 1980s

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Abstract

LOFTUS, K. H., M. G. JOHNSON, AND H. A. REGIER. 1978. Federal–provincial strategic planning for Ontario fisheries: management strategy for the 1980s. J. Fish. Res. Board Can. 35: 916–927.

A new management strategy for Ontario fisheries was addressed by a federal–provincial task force in 1974–76. It was initiated in an atmosphere of concern over the deteriorating status of fish stocks in Ontario, and indeed elsewhere in Canada. The task force published interim documents on "Goals and Issues," on "Mandates," and on "Objectives." These received limited distribution for criticism. This report summarizes the proposed "Strategy." Speaking generally, it has become abundantly clear that our traditional approach to fisheries management — *development-oriented, exploitive, open access* — is no longer appropriate in the 1970s and 1980s. That approach, together with the accelerating impacts of land and water uses that conflict with fisheries, has resulted in serious losses in our resource base, particularly during the past two or three decades. A new approach to fisheries management, characterized generally by *maintenance* in the north and by *re-*

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habilitation in the south is now essential. Much of the scientific and technical knowledge needed for the new approach is already available. To apply that knowledge, and to achieve the new knowledge and current data series necessary to its application, a major new initiative is necessary. That initiative, though costly in comparison to past levels of expenditure, seems easily justified in terms of the current economic value of the resources. Furthermore, additional values attributable to fisheries resources are now gaining wide acceptance; e.g. healthy fish communities are indicators of healthy aquatic environments. The new initiative will require more than just funding. It will require the evolution of different value systems, and of new and/or more explicit policies regarding

- — a new level of public participation;
- — a "user pays" policy in place of the free access philosophy of the past — to meet some of the increased cost of managing the resource;
- — more limited access and increased emphasis on protection in place of the open access, common property approach of the past;
- — explicit recognition that "experimental management" is needed to gain the new knowledge necessary to manage;
- — recognition that management of fisheries requires greater attention to environmental quality matters;
- — explicit allocation of those parts of the resource base available for commercial and for recreational use;
- — new working arrangements between fisheries agencies and other institutions.

Résumé

LOFTUS, K. H., M. G. JOHNSON, AND H. A. REGIER. 1978. Federal–provincial strategic planning for Ontario fisheries: management strategy for the 1980s. J. Fish. Res. Board Can. 35: 916–927.

Un groupe de travail fédéral–provincial a élaboré en 1974–76 une nouvelle stratégie de gestion des pêches de l'Ontario. Le travail débuta dans une atmosphère d'inquiétude face à la détérioration des stocks de poissons en Ontario, comme d'ailleurs dans le reste du Canada. Le groupe de travail a publié des documents préliminaires : « Goals and Issues », « Mandates » et « Objectives ». Ces rapports ont été distribués à un nombre limité de personnes qui en ont fait la critique. Le présent rapport est un résumé de la stratégie proposée. En termes généraux, il est devenu très clair que notre approche traditionnelle à la gestion des pêches, axée sur le *développement*, l'*exploitation* et l'*accès libre* n'est plus pertinente aux années 1970 et 1980. Cette approche, de même que les répercussions de plus en plus fortes des divers usages de la terre et des eaux créant un conflit avec les pêches ont entraîné des pertes sérieuses de notre fond de ressources, en particulier durant les deux ou trois dernières décennies. Il est devenu essentiel d'adopter une approche nouvelle à la gestion des pêches, caractérisée dans ses grandes lignes par le *maintien* dans le nord et la *réhabilitation* dans le sud. On possède déjà une bonne partie des connaissances scientifiques et techniques requises par la nouvelle l'approche. Une initiative d'envergure est maintenant nécessaire pour appliquer ces connaissances et en acquérir de nouvelles, ainsi que des séries de données courantes. Bien que coûteuse par comparaison avec les niveaux passés de dépenses, cette initiative semble facilement justifiable en fonction de la valeur économique actuelle des ressources. En outre, d'autres valeurs attribuables aux ressources halieutiques sont acceptées par un nombre de plus en plus grand; e.g., des communautés de poissons en bonne santé sont des indicateurs d'environnements aquatiques en bonne santé. La nouvelle initiative exigera plus qu'un financement. Il faudra qu'évoluent des systèmes de valeurs différents et qu'on élabore des politiques nouvelles et/ou plus explicites concernant

- — un nouveau palier de participation de la part du public;
- — une politique selon laquelle « l'usager paye » au lieu de la philosophie d'accès libre du passé — ceci afin de défrayer une partie des coûts de la gestion des ressources;
- — accès plus limité et plus d'accent sur la protection, au lieu de l'approche d'accès libre et de propriété commune du passé;
- — reconnaissance explicite du besoin d'une « gestion expérimentale » afin d'acquérir les connaissances nouvelles nécessaires à la gestion;
- — la réalisation que la gestion des pêches exige qu'on se préoccupe davantage des questions de qualité de l'environnement;
- — le partage explicite de parties de la ressource destinées à l'exploitation commerciale et à des fins récréatives;
- — nouvelles dispositions de travail entre organismes s'occupant des pêches et autres institutions.

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Introduction

Fisheries policies are being reassessed and redirected in many parts of the world, and especially in North America. Ontario has been one of numerous "hot spots" in the struggle for policy reform. The present statement derives from a group process that began in Ontario about 15 years ago, reaching high levels of intensity in 1974–77. In the course of these activities Ontario individuals have participated in other groups, seeking to create bases for new policies, at all levels of agency from very local to worldwide. The case of Ontario was always viewed as a policy microcosm more or less intimately related to other, larger policy macrocosms; in turn Ontario is the macrocosm to the more local regional and district microcosms. The proponents of the present statement feel that they have produced a statement of some relevance beyond Ontario, though of primary relevance to Ontario.

Ontario fisheries are a joint responsibility of both the provincial and federal governments. Furthermore, in the Great Lakes and connecting waters, responsibility for some fisheries resources is shared with the various state and federal government agencies of the USA. The higher level policy issues involved in such sharing of responsibility have not been addressed in recent decades with respect to Ontario fisheries and are not taken up in the present statement. Similar policy reforms are occurring in most or all of these agencies approximately in phase temporally; some kind of effective coordination is apparent. A relatively informal network of decentralized, laterally organized groups of scientists, managers, and resource users has been primarily responsible for policy reforms within these jurisdictions and for the coordination among agencies.

The literature relevant to fisheries policies is quite extensive, spanning a wide spectrum from the practical with local relevance, to theoretical, abstract generalizations. This is the case for Ontario fisheries as well as for those of some other jurisdictions. The following references are among those perceived as most immediately relevant by the 1974–77 strategic planning for Ontario fisheries: Loftus (1968); Loftus and Regier (1972); and Ricker and Weeks (1973). Other works that were initiated during the intense 1974–77 planning phase, and that are generally consistent with the contents of the present paper include Kerr and Lawrie (1976), Fisheries Research Board of Canada (1977), Colby (1977), Christie (1978), and Francis and Regier (1977).

Early in 1974 the Federal–Provincial Committee for Ontario Fisheries established a task force to assess the present status of fisheries and to recommend broad courses of action or strategy for the future. Much was known about the continuing deterioration of fisheries in Ontario because of pollution, overfishing, invasion of new fish species and other stresses (Ont. Min. of Nat. Resour. 1973; Loftus and Regier 1972). However, the Federal–Provincial Committee wanted a new, thorough analysis of all aspects of the Ontario fisheries, put together in an holistic framework. This report summarizes the results of these deliberations carried on under the title of Strategic Planning for Ontario Fisheries (SPOF).

The principal observations of the SPOF task force are examined under three components:

— societal goals related to the fisheries resource;
— public issues and basic problems in fisheries management in Ontario; and
— strategy for the future.

Before proceeding to the body of our report, however, there are several fisheries management principles or concepts upon which we wish to comment. Some of these are past guidelines which we believe must be replaced or greatly modified, for example, free open access to the common property fishery resource. Others are principles for the future, for example, healthy well-balanced fish communities as indicators of the quality of the human environment.

Gross overfishing has occurred worldwide because of perpetuation of free, open access to common property fishing resources. Only in recent years have we examined the historic record in Ontario and found the classic sequence of events commonly called the "fishing-up" process. Only with the loss of individual fish stocks, usually premium species like lake trout or lake whitefish, have we appreciated that the limits of fish stocks to accommodate for stress have been passed. Even now we delay and compromise over protection of Lake Erie yellow perch, Lake Ontario whitefish, and lake trout in many parts of Northern Ontario. We cannot count on self regulation of fishing effort because this effort is often partially diverted to other, usually less valuable fish stocks, while maintaining enough stress on valuable species to prevent their recovery. Alternatives to present management practices are examined in this report.

In effect, the fisheries resources of Ontario are held in trust for the public by government. The public can be regarded as "stockholders" of the resource since the fish belong to no one individual until caught. Many fishery resources are scarce in relation to demand and recreational and commercial fishermen compete among themselves. Under these circumstances there is little incentive for individuals to restrict fishing to maintain fish stocks or fishing opportunities. Individual conservation efforts are negated by stress placed on the resource by others. For example, in commercial fisheries there is always an incentive to build bigger and better boats, use more expensive and effective gear, or to allow new fishermen into the industry, until it is no longer profitable. The classic results are depleted fish stocks because of excessive exploitation and an overcapitalized industry which dissipates its profits to compete within itself. Furthermore, the value of the resource to the "stockholder" is depreciated and the costs of management, paid mainly by public taxes, continue to increase. Similar examples can be given with respect to other

stresses like pollution or recreational fishing. Means to reduce costs to the public at large, by establishing a "user pays" principle, are considered in this report.

Determination of maximum physical yield or maximum economic yield while sustaining the supply of fish has never been simple (Larkin 1977). In any event, instability of fish stocks and environmental changes have meant that these estimated limits, where they have been applied, were inadequate over the long term. Also, with few exceptions, the cost of these techniques is prohibitive for use in Ontario's many fisheries. We recommend development of a flexible new concept; optimum sustained benefits, a mix of employment, recreation, income and other benefits, according to stated public priorities.

The role of fisheries agencies in addressing environmental problems in Ontario is recognized by the Federal–Provincial Ontario Fisheries Committee. In the past, fisheries agencies have been concerned mainly with maintenance of fish harvest and allocation to fishermen. This has resulted in a lack of interagency coordination on common fisheries and environmental problems, for example, mercury and PCBs. In future, fisheries agencies have to play a more active role in decisions relating to water, land, and air where uses of these resources conflict with fisheries. Another reason for broadening our role is that a healthy, well-balanced fish community is an excellent measure of the quality of the aquatic environment and indirectly the human environment. In that sense, the loss or contamination of fish are concerns of society at large.

Broader environmental responsibilities for fisheries agencies are examined in this report. These require recognition of responsibility to society at large and not just fishermen. Some institutional changes are required, particularly in interagency coordination, although the extension of formal mandates for fisheries agencies may not be necessary.

The Federal–Provincial Committee for Ontario Fisheries is convinced that to achieve societal goals relating to fisheries and to resolve fisheries problems, major emphasis must be given to inducing changes throughout the whole system affecting fisheries. We must look beyond the shorelines of the province's lakes and streams. We must look deeper than the supply–demand characteristics of fish and fishing opportunities. To define desirable strategies we must understand and keep in mind both the goals of society and the major issues or basic problems to be resolved.

Conflicts in the value system, such as quality of the human environment vs. entrepreneurial fast-return, are fundamental to many issues. These issues will be resolved only through gradual evolution of the value system itself. Public awareness and positive, effective public involvement are required in fisheries management to understand and apply society's values in making management decisions. Future management should be balanced and comprehensive. It should concentrate on creating the future, not predicting it.

This report is offered as a baseline, a framework, for creating a new approach to fisheries management in Ontario. We recommend its adoption in principle by the governments of Ontario and Canada.

Societal Goals for Ontario Fisheries

Societal goals in this context are what people need and want from the province's fisheries resources. Fortunately, the SPOF task force had at its disposal several recent studies on recreational and commercial fishing in Ontario. It also assessed goal statements of the two fisheries agencies (see below) and found that they were mutually reinforcing. Out of this assessment came

- — a better understanding of the several kinds of value associated with fisheries;
- — an appreciation of the food, income, employment, and recreation now provided from fisheries; and
- — a new, more comprehensive set of goals which we believe fisheries agencies and governments should recognize.

1. Goals of the Fisheries Agencies

The federal Fisheries and Marine Service and the Ontario Ministry of Natural Resources have both developed statements of goals. For the Fisheries and Marine Service, MacKenzie (Ont. Min. Nat. Resour. and Environ. Can. 1974) explored potential alternatives for goals and goal frameworks. He examined goals stated by the Economic Council of Canada (17 in all), and formulated these into 3 categories and 10 goals.

(a) *Environmental Harmony*

Conservation and enhancement of the harvestable productivity of aquatic (freshwater and marine) ecosystems.

Understanding and control of the interaction of human society and the biosphere.

Development of an ecological conscience in society.

(b) *Material Well-Being*

Sustained growth in the regional economies.

Rising returns to production factors (capital, labor, and enterprise) and equitable distribution of same.

Increased employment opportunities (quantity and quality).

Economic stability (including trade and monetary affairs).

(c) *Cultural Opportunity*

Expansion of opportunities for recreation and personal development (including education and physical and mental health).

Maintenance of freedom and security (minimum social disruption).

Advancement of international peace and progress (national obligations to the world community).

The Ontario Ministry of Natural Resources has adopted an overall goal for the Ministry and three subgoals for its three official programs (Anon. 1972).

The goal of the Ministry is

To provide opportunities for outdoor recreation and resource development for the continuous social and economic benefit of the people of Ontario and to administer, protect, and conserve public lands and waters.

The subgoal of the Land and Water Management Program is

To administer, protect, and conserve public lands and waters; and to ensure with other agencies, through participation in planning and control, coordinated uses of all lands and waters.

The subgoal of the Resource Products Program is

To provide an optimum continuous contribution to the economy of Ontario by stimulating and regulating the utilization of available supplies of fish, furbearers, minerals, and trees by resource products industries.

The subgoal of the Outdoor Recreation Program is

To provide from public lands and waters and to encourage on other lands and waters.

A wide variety of outdoor recreational opportunities accessible to and for the continuous benefit of the people of Ontario.

The identification and conservation of unique or representative physical, biological, cultural, and historical features of the province.

A continuous contribution to the economy of Ontario from tourism and its related industries.

MacKenzie's independent articulation of goals for the Fisheries and Marine Service and those developed for the Ontario Ministry of Natural Resources are quite similar and are compared below. (The additional material in the OMNR list, which was not contained in the goal and subgoals above, are from the statements explaining the goal and subgoals as they appear in the original document (Anon. 1972).

Comparison of FMS and OMNR Goals

FMS	OMNR
Environmental Harmony	*Land and Water Management*
— conserve harvestable productivity;	— protect capability and productivity of public land and water;
— control interaction of society and biosphere;	— ensure harmonious pattern of uses.
— develop ecological conscience.	
Material Well-Being	*Resource Products Management*
— regional economic growth;	— sustain community economies;
— increased employment;	— contribution in jobs provided;
— returns to production;	— contribution by resource products industry;
— equitable distribution;	— optimum contribution within constraints.
— economic stability.	
Cultural Opportunity	*Outdoor Recreation Management*
— recreation and personal development;	— recreation, man's understanding and appreciation;
— freedom and security;	— wide variety of opportunity;
— international peace and progress.	— tourism.

2. Why are the Fisheries of Ontario of Value?

Basically they satisfy public needs and wants. For example, people *need* food, employment, and a minimum level of environmental quality; these are essential. In addition, people *want* abundant, high quality food; fulfilling employment; high environmental quality; diverse outdoor recreational opportunities, and institutions that provide for protection and well-being. Fish, the aquatic habitat, and governments as custodians of the fishery resource are the elements of the system that provide and allocate these benefits to satisfy in part society's needs and wants. Government has recognized for several years now that, especially in southern Ontario, we have a deficit of supply.

3. What Benefits do Fisheries Supply?

As of 1973 public surveys indicated that an estimated 38% or 3 million of the province's 8 million people went fishing annually (Government of Ontario 1974a, b). Furthermore, 20–25% more opportunities to fish were desired by Ontario anglers. In terms of outdoor recreational activities in which Ontario residents would like to participate more frequently, fishing ranked number 2 behind swimming and ahead of golfing and camping. Lack of nearby opportunities, poor quality, and crowded facilities were more serious constraints to participation than was cost. A survey of resident and nonresident anglers licensed in 1970 indicated that angling accounted for over 43 million days of recreation annually, with a catch of about 30 million fish (Cox and Straight 1975). This amounted to an estimated 35 million pounds of fish, most of which was eaten. Anglers spend over $300 million pursuing their pastime.

Commercial fishing in Ontario produces the largest

quantity of freshwater fish in Canada, the harvest being 40 million pounds of fish with a gross value of $20 million and a return to fishermen of $10 million (Adams and Kolenosky 1974). Full and part-time employment totals over 4000 fishermen, with 900 additional people in handling and processing. Additionally, there are 2000 baitfish operations in Ontario, producing 90 million baitfish with a *wholesale* value of about $2 million. In many areas of Ontario there is a great shortage of baitfish in the summer months.

As for fish watchers, scuba divers, and other nonconsumptive users of fisheries, there is little quantitative information available. However, over 120 000 people visit the 14 fish culture stations annually and one provincial fishway on the Saugeen River attracts more than 20 000 sightseers each year. Greater emphasis should be given to nonconsumptive uses in future. These uses will provide recreational benefits and at the same time allow greater protection of the resource.

None of the above touches upon the ancillary demand for goods and services to supply anglers, commercial fishermen, and other fish-oriented users. The demand for fish and fishing opportunities produces a secondary demand with important economic and employment ramifications, *generating tens of millions of dollars in cash flow to local economies and tens of thousands of full and part-time employment opportunities.*

4. What are Societal Goals That Relate to Fisheries?

We can summarize briefly the elements that need to be recognized in a formal statement of societal goals. These elements are

- a healthy human environment;
- an abundant supply of fish for food;
- fish fit for human food;
- employment and income;
- recreational opportunities;
- harmonious use; and
- knowledge of the importance of the fisheries and the values and principles required for rational management.

Before presenting our two formal goals, there are three observations to be made

- Society has not yet been given opportunity to review the goals, to understand their implications, and to consider the use that may be made of them. Thus until society has a chance to respond to these statements, they should be considered as goals *for* society rather than goals *of* society.
- The goals and their elements are interrelated and should be viewed as a set or a system.
- Failure to protect the biological productivity of the fisheries resource, or in broader context, failure to maintain healthy aquatic ecosystems, ensures that few of society's goals for fisheries can be met. Without the resource there can be no benefits, no alternatives, no strategies, and no need for fisheries management. In other words, resource protection must come first and allocation second.

The formal statement of societal goals for fisheries is as follows:

- to protect and maintain healthy aquatic environments and associated fish communities, and to rehabilitate those now degraded, to ensure continued supplies of fish and fishing opportunities which in part satisfy society's requirements for:
  - wholesome food;
  - employment and income;
  - recreational activity; and
  - high quality of the human environment;
- to create public awareness of the importance of healthy fish communities and aquatic ecosystems, and to engender a harmonious pattern of uses of fisheries resources and the terrestrial and aquatic ecosystems upon which they depend.

Issues in Fisheries Management

Defining and assessing publicly perceived issues and underlying problems that prevent the achievement of goals is a necessary step in determining strategies. Accordingly, a thorough review was made of legislative debates, government reports, the scientific literature, and the experience of knowledgeable fisheries staff. Two important generalizations have come to light as a result:

- To define and understand fisheries problems and issues, a larger system must be considered. This system includes, among other components, fish communities, aquatic environment, fishermen, polluters, conflicting users of land, water, and air, and fisheries agencies themselves.
- When stocks of fish become extinct or rare and when fish become unfit for food because of contamination with dangerous chemicals, this is a clear sign that the human environment is deteriorating. We believe that it requires a major initiative to deal not only with issues or symptoms (such as loss of income and recreational opportunities), but also with problems such as lack of public awareness and ineffective institutions.

We have grouped public issues into three categories:

- loss of fish and fishing opportunities;
- loss of environmental quality; and
- conflicts among users of the environment and the fishery resource.

The basic problems underlying these issues also fall into three groups:

- lack of public awareness and involvement;
- inadequate scientific and technical knowledge;
- ineffective institutions.

1. Loss of Fish and Fishing Opportunities

Growth of population and the economy in Ontario has been attended by progressive loss of fish stocks.

Fish communities have been degraded by one or more stresses including pollution, overfishing, habitat destruction, and invasion of pest species such as smelt and sea lamprey. Efforts by fisheries agencies to halt or reverse the depreciation have, with a few exceptions, been too little and too late. Recently, however, new knowledge has bcome available that has advanced our understanding of how various stresses affect fish stocks (Loftus and Regier 1972). This offers a basis for cautious optimism that depreciated fish communities can be rehabilitated.

In the past, fisheries management policy has concentrated on the supply of fish, using mainly biological guidelines. We now recognize that principles from the economic and social sciences are equally important in solving problems associated with the open, free access nature of the resource. Fisheries are neither free nor inexhaustible. They have a potentially great economic value which tends to be ignored because little or no rent is charged for their use. They have a significant additional value that cannot be measured in economic terms as implied in our discussion on societal goals. Under present policy, without a "user pay" principle, there is a sizeable cost to society at large for their management, a management that is still ineffective. Failure to adopt strategies that reflect the true value of Ontario fisheries is certain to test the capacity of the resource to survive.

Elements of this issue include
- — loss of employment and income in commercial enterprises;
- — loss of fishing opportunities now and for future generations;
- — extinction of fish stocks and genetic material;
- — inequity and inefficiency in allocation of the resource;
- — regional variations in potential fish harvest;
- — inadequate attention to factors affecting demand.

2. Loss of Environmental Quality

Aquatic systems essential for healthy fish communities continue to be impaired because of the growing and conflicting demands for alternative water uses. Particularly for recreational fishermen, high environmental quality is itself an objective, a benefit, something desired as part of the fishing experience. Because we have so much water in Ontario, in the past we gave little thought to restricting its use. Nowadays we realize that water for fisheries and for human consumption are two of the most sensitive uses. In future the public must become aware that healthy fish communities and aquatic ecosystems serve as a "barometer" for human health and well-being. Fisheries agencies must deal with environmental issues to safeguard fish stocks and fishing opportunities. From now on, we believe that fisheries agencies also must recognize a broader objective than providing fish, and acknowledge a responsibility to maintain a healthy aquatic environment as an indicator of the quality of the human environment.

Elements of this issue include
- — public health problems;
- — aesthetic deterioration and poor quality fishing experiences;
- — inadequate guidelines for allocating water among competing uses;
- — endangered aquatic communities and species and stocks of fish; and
- — inadequate water quality standards and their enforcement.

3. Conflicts Among Users of the Environment and the Fisheries Resource

Alternative uses of the environment can affect fisheries directly or indirectly. Examples of direct conflict are toxic pollutants, contamination by mercury or PCBs, and the destruction of fish in power stations. Indirect conflicts include dam building, gravel removal from spawning areas, pesticide use in agriculture, urban, and industrial development. Resolution of these conflicts is essential if high quality fisheries are to be maintained and restored. If resource allocation conflicts cannot be resolved by giving priority to the most sensitive uses such as fisheries, fisheries management programs will be wasted in the long term.

In addition to conflicting competitive uses of the environment, conflicts arise among fishermen. If demand is allowed to grow, conflicts must increase in the face of limited supply. The 44 million surface acres of water in Ontario are capable of producing 100–200 million pounds of fish annually. Some conflicts are not even true competition for the same fish stocks but rather lie in differences in value systems among the parties in disagreement. Unfortunately, such "imaginary" conflict can become a public issue at the local level and consume much time and energy of fisheries agencies.

Elements of this issue include
- — direct water use conflicts;
- — indirect conflicts;
- — native people vs. other fishermen;
- — commercial vs. sport fisheries;
- — resident vs. nonresident anglers.

4. Lack of Public Awareness and Involvement

A basic problem in fisheries management is the lack of a stated value system on which the majority of the public and fishery administrators agree. At the moment many of the values held to be important by users of the fisheries and the environment are incompatible with the maintenance of fisheries resources.

If fisheries resources are to exist in abundance and quality in future, the public and fisheries agencies must generally agree on a new value system. As we see it, the public first must become aware of the nature and importance of fish communities and aquatic ecosystems. The public requires information also with respect to both traditional and new values to form their own value

system, which in turn needs to be communicated to government and fishery administrators. Means to weigh conflicting values and mechanisms to define priorities are required. For example, is it more important to safeguard fish as food over the long term or to allow pollution for short-term profit?

Commonly, most problems tackled by government are approached from a technological viewpoint. More or different goods and services solve the problem. However, we now realize that there are no technological solutions to nontechnological problems. Ethical considerations require priority. Are free, open access to exploitation "and freedom to pollute" alternatives when it is part of the human environment that is being destroyed?

These questions have caused governments to explore new communication channels, for example, to review major policy options, but better methods are needed. How can we communicate with and listen to the public at large to achieve understanding of contemporary and changing values? Strategies and tactics will likely evolve best through a controlled, adaptive process. The dialogue created should offer the public an analysis of alternative values. It should also serve to communicate and seek agreement to rational, scientific principles for management, principles from the economic and social disciplines as well as ecology.

Elements of this basic problem include
- — conflicting, intuitive value system;
- — inadequate environmental conscience;
- — ineffective communication among people and governments;
- — lack of public knowledge of the importance of fisheries; and
- — of aquatic ecosystems and the principles of management.

5. Inadequate Scientific and Technological Knowledge

Science and technology mutually support each other in providing new understanding, principles, and techniques for management. The knowledge gaps that now exist are many and require attention across a wide spectrum of disciplines, especially ecology, economics, and the social sciences. Progress is not likely to be made uniformly in every field of expertise. Present shortfalls in ecological knowledge include
- — understanding and modeling stress effects on fish and aquatic communities to improve predictive ability;
- — basic inventory and analysis of baseline conditions in unstressed systems; and
- — examination of important concepts relating to fish and aquatic systems such as stability, diversity, and resilience to disturbance.

Technological improvement in fishing gear is needed in selective harvest of desired species while at the same time protecting others, in decreasing conflict and interference among commercial fishermen and anglers, and in artificial growing of fish (aquaculture).

Economic understanding of Ontario fisheries, especially recreational fisheries, has been described as a vast wasteland. Decisions with respect to allocation and subsidization are commonly made without adequate knowledge of the potential economic benefits, if any. A knowledge of economic principles and a system for providing basic economic data would greatly assist in defining trade-offs between alternative users. Economic studies are required to understand market structures and to predict future recreational and commercial requirements. Similarly, fisheries problems require research in the field of the social sciences, in areas of culture and behavioral conflicts.

It is doubtful whether educational programs for fishery specialists are of sufficient strength. Certainly research is inadequate on interdisciplinary lines, among biologists, economists, and social scientists working together on complex problems.

Elements of this basic problem include
- — biological and physical components of the aquatic ecosystem;
- — technological requirements for optimum exploitation of aquatic resources;
- — economics;
- — social forces related to fisheries;
- — research and training relative to Ontario fisheries; and
- — information collection and distribution system for management.

6. Ineffective Institutions

The depressed state of the fisheries and the issues and problems summarized above are evidence that decision-making processes of the past and present do not adequately serve the public or fisheries agencies. The complexity of constitutional jurisdiction over natural resources impedes sound short- or long-term management. Thirty-two agencies, 19 federal and 13 provincial, have legislation and programs that affect the management of Ontario fisheries (Ont. Min. Nat. Resour. and Environ. Can. 1975). It is not the number of agencies so much as the lack of interagency coordination that is the problem. Another facet is the lack of involvement in the decision-making process of many concerned groups who should be considered.

Most decision-making has not been based on forward-looking multidisciplinary analysis of the full breadth of objectives and strategic alternatives. Much decision-making has been reactive, aimed constantly at old problems rather than at exploiting new opportunities and avoiding future problems. Further, it has been slow and cumbersome. Results are not usually adequately measured or evaluated. Older ineffective programs have blocked newer innovative approaches. Generally, managers have had little formal training in management

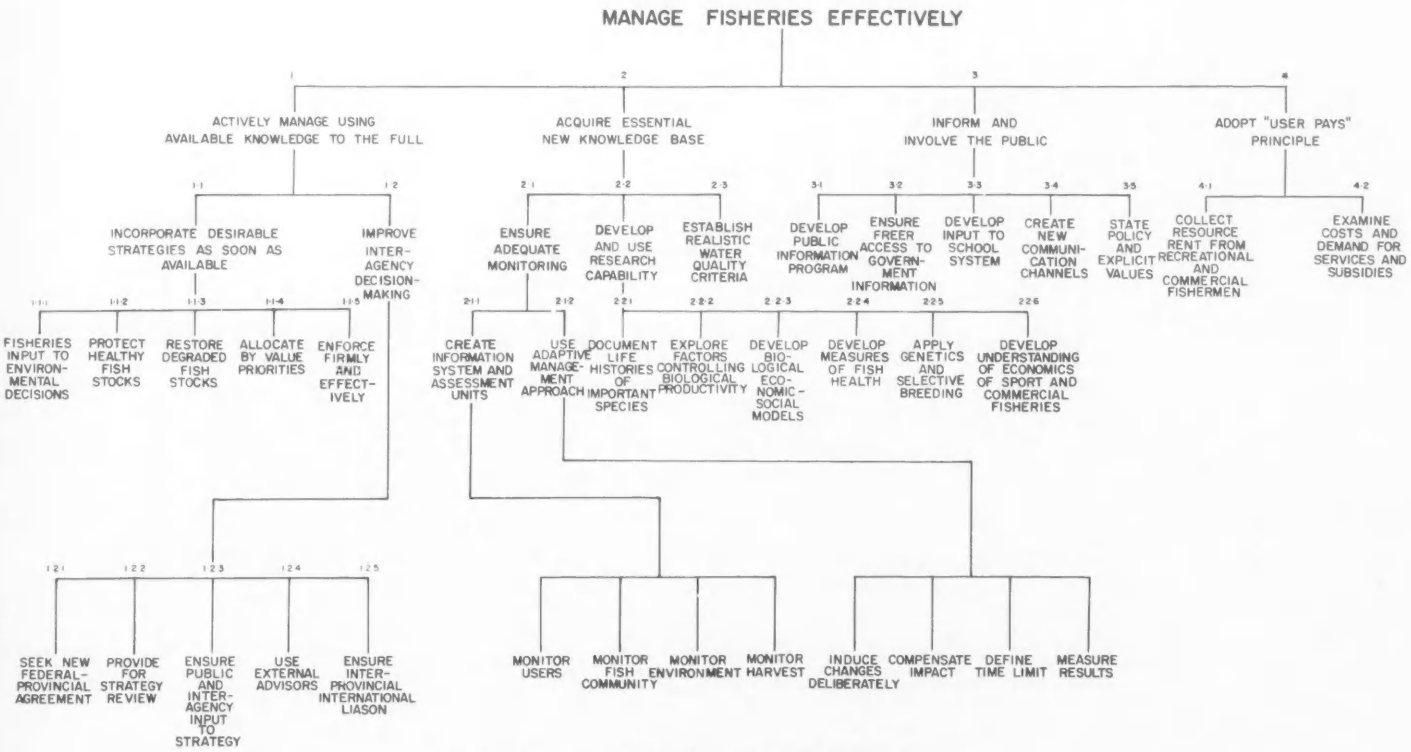

FIG. 1. Strategy tree for effective fisheries management.

techniques. Enforcement activities appear to receive little support for tackling large, complex cases.

Elements of this basic problem are

— inadequate government policy and legal framework;
— inadequate managerial systems and decision-making processes;
— ineffective interagency planning and program delivery; and
— lack of will to enforce resource protection regulations.

Strategy for Ontario Fisheries

Helping society to attain its goals with respect to fisheries and to resolve issues and problems requires a new approach to managing fisheries. Many of the strategy elements identified below are quite different from present management practices. We strongly urge that the elements be considered as a set, a management system. For example, new management capability and the acquisition of essential new knowledge require increase in revenues ("user pays" principle). Public support for active intervention will require public awareness and involvement. In our view, this strategy or a derivative of it is the option of choice compared to present management.

In developing the strategy elements, we found that they formed a hierarchy, with major and subordinate levels. Thus, in Fig. 1, the strategies are presented in the form of an inverted tree. Although not shown, the tree should be regarded as having an open-ended structure to allow adding new levels, for example, tactics or operational details appropriate to regional or local concerns. If the strategy is approved in principle, one of the next steps in the management process will be to develop tactical plans, for example, for the Ontario waters of the Great Lakes.

We recommend the adoption of four primary elements for the effective management of Ontario fisheries:

1. Using available knowledge to the full to manage fisheries and conflicting uses of the environment more effectively.
2. Develop the new broader knowledge base essential for more effective future management of Ontario fisheries.
3. Create an aware public and develop mechanisms for positive and effective public involvement in management decision-making.
4. Adopt a "user pays" principle and capture from the users of the fishery a resource rent that reflects more rationally the value of benefits received and the true cost of future effective management.

These primary strategy elements have been broken into subordinate elements as outlined below.

1. Manage fisheries more effectively, using available knowledge to the full.
   - 1.1 Ensure that management practice incorporates desirable strategy elements as soon as they become available.
     - 1.1.1 Ensure that environmental quality criteria essential to the health of components of aquatic communities are being met by providing input to agencies who establish them, by monitoring relevant water quality parameters, and by insisting on appropriate action by the environmental protection agencies when criteria are not met.
     - 1.1.2 Prevent overfishing of *undegraded* aquatic communities by monitoring individual stocks and the community for signs of stress and adjusting harvests accordingly.
     - 1.1.3 Rehabilitate *degraded* communities as far as possible towards their original self-producing stable state by reducing identified stresses and planting hatchery raised fish of native species or, as an interim measure only, of exotic species.
     - 1.1.4 Ensure that allocation of allowable yields among competing users is based on ongoing appraisal of society's values regarding use of the fishery resource; develop adequate criteria based on publicly accepted biological, economic, and social values regarding alternative uses.
     - 1.1.5 Enforce all management rulings consistently, equitably, and effectively.
   - 1.2 Strengthen interagency coordination and decision-making mechanisms.
     - 1.2.1 Develop a new Federal–Provincial Agreement for the management of the fisheries.
     - 1.2.2 Create an ongoing process for strategy review between Ontario Ministry of Natural Resources and Canada.
     - 1.2.3 When appropriate, ensure representation of the public and other federal and provincial agencies in strategic planning for fisheries.
     - 1.2.4 Ensure the best use of available talent external to the two governments by incorporating advisors from municipal governments, university departments, and institutes.
     - 1.2.5 Ensure close liaison interprovincially and internationally to develop rational joint programs.
2. Develop essential new knowledge base for more effective future management.
   - 2.1 Establish adequate systems for collection, analysis and reporting of relevant fisheries information on a real-time basis.
     - 2.1.1 Create capable fisheries assessment units to monitor events in representative fisheries and ensure prompt input of user, fish community, environment, and harvest data generated to an Ontario Fisheries

Information System having storage, retrieval, and analytical capability, accessible province-wide. Trend-through-time data will be valuable in examining policy implications, for example, to explore usefulness of principles like economic efficiency in commercial fishing.

2.1.2 Use an adaptive or experimental management approach where necessary and pay the costs of social and economic dislocation, especially where existing information is not adequate for decision-making and a substantial risk of imminent irreversible fishery collapse evidently exists.

2.2 Develop new fisheries theory and methodology through practical and innovative field and laboratory research in biology, economics, and the social sciences.

2.2.1 Describe the life histories of significant aquatic community components defining their distribution in time and space and devising methods to sample them; estimate their recruitment, growth, and survival rates; and clarify their interrelationships.

2.2.2 Define the mechanisms determining fisheries productivity in unstressed communities and evaluate the influences of such stresses as exploitation, cultural developments, and introductions of exotic species into watersheds.

2.2.3 Make use of existing data and theory to create simulation models of aquatic communities and the fisheries dependent on them to define management measures likely to result in optimum sustained benefits in the biologic, economic, and social sense.

2.2.4 Develop new approaches to evaluating the health of aquatic communities based on such emergent properties as community, stability, diversity, size–density relationships. These may provide simpler, cheaper, less data-intensive models on which management can be based.

2.2.5 Apply modern genetic theory to (a) develop a better understanding of the dynamics of wild fish populations, (b) further the use of selective breeding as a means of improving the performance of hatchery supplements to wild stocks, and (c) as a means of furthering the profitability of fish farming.

2.2.6 Develop an understanding pertinent to Ontario of the economics of recreational and commercial fishing, including the interrelationships with ancillary service industries and the economic impacts of changes in managerial practices.

2.3 Conduct the necessary monitoring and assessment to establish realistic water quality criteria ensuring optimum survival, growth, and reproduction of the essential components of aquatic ecosystems.

3. Create an aware public and develop mechanisms for positive and effective public involvement.

3.1 Create or strengthen information services particularly at the local level.

3.2 Develop mechanisms to allow the public freer access to government information.

3.3 Actively provide input to the school system with respect to the values associated with fisheries resources and the ecological, economic, and social principles required for rational management.

3.4 Create and institutionalize new communication channels among fishermen, the public at large, and fisheries agencies.

3.5 Put emphasis on the development of policy statements that spell out the values and principles that need to be recognized in fisheries management.

4. Adopt a "user pays" principle in line with the value of the fisheries resource and the true cost of effective management.

4.1 Collect a resource rent from recreational and commercial fishing interests, through license fees, resource royalties, or other appropriate mechanisms.

4.2 Given that governments have invested heavily in recreational fishing services and in subsidies and services to the commercial fishing industry, ensure that governments examine and understand the dimensions of demand in relation to the cost of supply.

The broad strategy presented here, in our judgement, is the best and perhaps the only alternative to what we have been doing in fisheries. Within this framework, optional tactics will require careful selection. We wish to communicate our sense of urgency. Current program delivery in Ontario will likely result in continued loss of fish stocks, and in the consequent loss of options available for future management action, unless decisions are made soon.

Postscript

The foregoing interagency statement, except for the first few paragraphs of the introduction, was completed in April 1976. A multistage process to test the statement for adequacy, relevance, and practicality was then initiated. The stages were as follows:

— test for tentative endorsement by the deputy ministers at both provincial and federal levels;

— test for tentative endorsement by the appropriate Ministers;

— convene regional meetings of administrators and fisheries experts in the Ministry of Natural Resources to communicate the contents of the document and to achieve measurable reaction to its several components;

— convene regional meetings as above but with representatives of the public;

— undertake presentations to special interest groups, e.g. Ontario Federation of Anglers and Hunters (Executive and Zone meetings), Ontario Council of Commercial Fishermen; Canadian National Sportsmen's Shows, Outdoor Writers of Canada, etc.;

— reassess the strategy in response to comment and present again to the Minister of Natural Resources and his advisors;

— if directed, present the strategy to appropriate Cabinet committees for consideration and action.

Much experience useful to the effective communication of rather abstract material has been gained during the foregoing process. Perhaps most important was the development of an historical context and some lake "case histories" as a background against which to present the proposed strategy.

As of January 1978 the process has been completed in Ontario and the proposed strategy has emerged from the multistage process, virtually intact.

Acknowledgments

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Harvesting Polluted Waters: Waste Heat and Nutrient-Loaded Effluents in the Aquaculture. *Edited by O. Devik. Plenum Press, New York and London, 1976. xi + 324 p. $29.50.*

Harvesting Polluted Waters is Volume 9 in the Environmental Research Series, sponsored by the Special Program Panel on Eco-Sciences, a body of the NATO Science Committee.

Dr O. Devik sets the context for this book as assessing improvements in the efficiency of recycling solid and liquid wastes, through judicious use of photosynthesis in combination with waste heat. This topic is addressed by twenty contributors, largely from Scandinavia and Atlantic North America. Only two participants are from outside the rim of the North Atlantic. Not surprisingly, this results in a bias towards problems of marine aquaculture in the north temperate zone, a context somewhat more specific than the book title would indicate. The bias is unfortunate in one sense, for most of the successes in coupling sewage effluent to aquaculture are found in tropical freshwaters.

Considering the purpose of the book, it is surprising how few of the papers deal with actual cases of the use of heat or nutrient effluents in aquaculture. Only one paper deals specifically with the use of heat, in this case to speed the development of Atlantic salmon to the oceanic stage. Nevertheless, this experiment contributes substantially to the understanding of problems associated with the use of heated water. Similarly, only two papers deal with actual attempts to utilize nutrients in aquaculture; one describes the entrainment of water masses in plastic cylinders to create "marine greenhouses." The other describes raceways in which sewage effluent is mixed with seawater and coupled to an integrated aquaculture of algae, oysters, and benthic worms. These three papers, together with a review on the technical production of microalgae and a paper on factors influencing growth and feeding in bivalves, form the backbone of the book as it relates to effluent-enriched aquaculture.

Of the remaining papers, four are stimulating though somewhat peripheral. Two of them encourage us to consider dialysis techniques and the culture of angiosperms as systems that could be coupled to nutrient effluents. The other two deal with ecological processes that bear on effluent aquaculture. At the micro level, we learn how the filtering process in crustacean and bivalves contributes to stability in phytoplankton communities, and at the macro level, how the choice of a mariculture system is influenced by the physical, chemical, and biological characteristics of coastal (albeit Norwegian) waters.

A point made frequently throughout the book is the problem raised by the temperate zone climate. While the production rate of nutrient effluent tends to be nonseasonal, the other variables important in effluent aquaculture, namely the ambient water temperature and the photosynthetic rate, are high only during a 4–5 month growing season. Although this problem seems to be a persistent stumbling block to the coupling of effluents and aquaculture, one can find no analysis of it in the book. The generality of the constraints leads one to wonder whether temperate zone aquaculture, if it is to incorporate nutrient and heat effluent, should be based on a heterotrophic, rather than an autrotrophic production system, or alternatively, whether the aquaculture system should be based on some principle of foddering, which is normally practiced in the husbandry of terrestrial herbivores.

This collection of papers gives one the impression of a singular approach towards effluent aquaculture. To a food chain yielding commercially valued species such as oysters, salmon, or lobsters, effluents are added on the assumption that the rate of production will be stimulated. While this approach makes sense economically, and would lead to rapid incorporation of Research and Development findings by the private sector, it may be that this is not the most feasible approach biologically. For example, a point made by several contributors is the problem of control of phytoplankton growth rate, density, and species succession, when nutrient effluents are used to stimulate an extant food chain. In other words the structure of the food chain is altered as well as the rate variables. If this oversimplifies much of the current thinking about effluent aquaculture, it is to make the point that alternative strategies of system design are not examined in this book. For example, an alternative approach might be to link food chains to effluent on a step-by-step basis, starting with the effluent characteristics and adapting trophic links to it. The criteria for optimization might be the efficiency of nutrient recycling, energy utilization, or productive capacity. Here the goal would be insight into the problems of fertilizing an aquaculture system, rather than economic viability.

It may be unfair to say that a number of contributions to this book fail to deal directly with the central theme. Judging from the paucity of references to actual mariculture systems that use nutrient or heat effluent, it appears that little work has been done in this area and the field is very much in its infancy, at least in the Atlantic rim countries. Perhaps less excusable is a lack of reference to the considerable experience of Eastern European nations with pond fertilization, and Russian experiences with the use of waste heat. Similarly, there is little analysis of aquacultural practices in Taiwan, China, or Indonesia where the use of sewage is well advanced. While it is acknowledged that this symposium was directed primarily towards marine aquaculture systems, it seems unlikely that nothing could be gained by considering information from freshwater systems.

This book was not intended to answer all problems concerning the use of heat and nutrient effluent in marine aquaculture. It does bring attention to the potential possibilities, and it does serve to indicate that the state-of-the-art is in its infancy in the western countries. It does not contain the generality which would recommend it to students of aquaculture, nor is there the consistency in depth and quality of the contributions which would place it on many researchers' shelves. Nevertheless, a number of the articles are important contributions, and they make a trip to the library a requirement for anyone interested in the use of effluents for aquacultural purposes.

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(R173)

Aquaculture Practices in Taiwan. *T. P. Chen. Fishing News Books Ltd., Farnham, Surrey, England, 1976. xiii + 162 p. £5.00 (paperback).*

With a production of 114 thousand tonnes in 1974, Taiwan is certainly the world leader in per capita aquaculture production (>7 kg/capita compared with <3 kg/capita for China, <0.8 kg/capita for Japan and <0.2 kg/ha for the United States). In his handy little book T. P. Chen has neatly and concisely summarized the techniques used to obtain this production.

Milkfish, carps, tilapia, oysters, eels, and meretrix clams make up over 90% of the production and value of Taiwan aquaculture output and a major portion of this book has been devoted to the cultural practices of these species. However, other species, such as snakehead, walking catfish, mudskipper, and *Gracillaria*, the culture of which is unique to Taiwan, have not been ignored. In total the aquaculture of 18 species of fish, 5 species of molluscs, 4 species of crustaceans, an amphibian, a reptile, and one species of algae are presented in the 18 brief chapters.

For each species, Chen presents a brief history of the culture of the particular organism in Taiwan, discusses the methods used for production, identifies major problems, and provides a short list of pertinent references. The book is detailed enough to be almost an operating manual of culture procedures for the various species and provides such valuable tidbits of information as "If bitten, placing the turtle back into the water will cause it to release its hold."

Chen concentrates on culture techniques and gives us only a vague look at such aquaculture components as industry infrastructure, marketing, economics, government responsibilities, and extension work. It would have been interesting if such factors had been discussed since they are undoubtedly important to the success of aquaculture in Taiwan. Another unfortunate omission is the failure to include an index.

In the introduction Chen mentions what may be the most important difference between aquaculture in Taiwan and aquaculture in other parts of the world and that is "There is literally no gap between research and commercial operation. . . . The moment they (the farmers) learn that some new techniques have been developed or some new species have been introduced by the research institutions, they immediately flock to the institutions for information and request demonstrations." Would that were true in all countries.

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(R135)

Fishexpo '76 Seminar, Report of Proceedings, Melbourne, 21–23 Sept. 1976. *Convened by H. E. Rogers. Australian Government Publishing Service, Canberra, Australia, 1977. xii + 762 p. $13.00 (Australian).*

As in similarly organized seminars in North America these proceedings concern themselves primarily with the problems associated with the fishing industry of the country of the seminar's origin. This does not in any way diminish the value of the information presented to observers from other regions of the world; indeed, it can provide a valuable insight into problems that in many respects closely parallel those that exist in the fishing industries of many other countries.

The exposition was organized and promoted by the Fisheries Division of the Commonwealth Department of Primary Industry in cooperation with the Fisheries and Wildlife Division of the Victorian Ministry for Conservation. Its subject matter broadly encompasses the production, processing, and marketing of fish from Australian waters.

This prodigious document is organized as a series of 10 sessions constituting 42 papers. Each session is followed by a discussion of its included papers led by the session chairman.

The first two sessions deal with developments in fishing boat design and construction methods and materials, navigational and fish detection techniques, the use and degree of success of different types of gear and fishing methods, and the prospects for expansion of the fishery. It was felt that this will be determined not only by the success of exploratory fishing but also by the extent of the availability of facilities for processing deepwater species and the potential for increasing market demand. The feeling that rises to the surface in these two sessions is the very real concern that in Australia, the fishery is faced with the imminent management and jurisdiction of its 200-mile offshore coastal zone. The potential to maximize the opportunities that go with this responsibility are heavily dependent upon the means to provide the level of equipment sophistication and technical expertise to develop, exploit, and manage the resource.

The central theme of sessions three and four is the general state of quality control of fish and recommendations for improvements. The frequent questionable quality of fish in the Australian industry (a problem common to most fishing nations) is discussed. Shortcomings in retail handling methods, bacterial spoilage mechanisms and methods of control, the frozen storage stability of mechanically separated flesh, quality control imperatives of the fish canning industry and those recommended for the prawn industry are included. Also included is a dissertation outlining the need for training processing staff in basic quality control procedures.

What I find dismaying about this subject is the amount of accumulated knowledge concerning spoilage mechanisms and product quality loss and the difficulty of communicating this knowledge and its potential impact on the consuming market between the experts and many segments of the industry. It is also evident from the discussion that follows these sessions that there is a lack of agreement concerning with whom the responsibility and administration of quality control lies – a familiar but imprudent vacillation.

Sessions five through nine are concerned generally with the marketing of fish. The first two of these, sessions five and six, concentrate on attempting to evaluate and define restaurant and supermarket fish requirements and the changing attitudes and consumption patterns of the consumer. Included here are surveys that reflect consumer attitudes towards purchasing fish and statistical price trends of Australian fish. An observation worthy of note here is the factor prominent in surveys carried out in the U.S., the U.K., and New South Wales, the consumer's obsession with

freshness – the usual coincident of quality.

Fish in the fresh (nonfrozen) form appears to have the greatest consumer popularity. Improvements in communication between the fisherman, producer, and retail organizations and improved continuity of supply of fresh fish are voiced as being important factors influencing the increased use of Australian-caught fish in their domestic market.

The remaining three sessions, seven through nine, cover a review of distribution patterns of canned, frozen, and fresh (nonfrozen) fish in the Australian market; export marketing opportunities and problems; discussions of the possible advantages and disadvantages of government in seafood marketing; the operation and organization of a statutory seafood marketing organization and a commercial fisherman's association; proposed marketing policies and, finally, proposed promotional strategies in fish marketing.

Notwithstanding the lack of accord of various factions regarding any role the government may play in marketing, the impact of New Zealand's ongoing promotional activities, not to mention the success of the U.K.'s whitefish authority, in generating an awareness of fish as a primary staple was recognized as a positive contribution. What is particularly notable in their program is the cooperative attitude between the Fishing Industry Board (F.I.B.) and the industry. This should be regarded as a lesson in communication.

In summary, it is evident from the predominance of marketing-oriented subject matter in these proceedings that industry and government are conscious that the survival and progression of the industry hinges largely on its ability to improve the consumer image of Australian fish to displace a greater proportion of imported seafoods with domestically produced product and generally increase consumer acceptance of seafoods.

In general, the content of these proceedings are relevant to and cognizant of the problems inherent to the fishing industry today. As such they will be of interest to a wide cross section of those associated with the industry, from marine engineers to resource managers and food science and technology workers to marketing personnel.

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(R185)

Pacific Seashores: A Guide to Intertidal Ecology. *Thomas H. Carefoot. J. J. Douglas Ltd., Vancouver, B.C., 1977. 200 p. $12.95.*

This is a long-awaited book. With its glossy cover photograph, internal gallery of striking photography, and superb black and white illustrations by Doug Tait, this appears at first to be yet another of those seashore books aimed at the general public. A glance at the table of contents quickly shows that mercifully it is not. If one excludes the three very competent introductory sections (an introduction, the geological evolution of shorelines, and a discussion of water, waves, currents, and tides), and the three final chapters which appear to be tacked on (mariculture, pollution, and sand dunes), what remains is a serious attempt at describing the present state of shoreline ecology on the Pacific coast.

It's about time. The number of intertidal studies done on the coast of B.C. and adjacent waters is now very large. Much recent interest has been generated by the establishment, at last, of a Canadian marine station at Bamfield, by the establishment and proposed establishment of marine parks and by the high probability that there will soon be a lot of oil in these waters. Yet the literature has remained scattered in journals and theses, with a few of the more important concepts showing up in textbooks of ecology. Because it uses a process-by-process format, rather than species-by-species or habitat-by-habitat, this is the first book of its kind.

The three central chapters are "distribution of organisms on the shore," "the causes of intertidal zonation," and "the economy of the shore." The theme produced by organizing the material this way mirrors the history of the subject, from zonation through population ecology to systems ecology. In the first of these chapters the author presents the phenomenon of zonation, relying on the descriptive universal scheme of the Stephensons. Then he discusses some of the older theories that were advanced to explain it, such as Doty's idea of critical tide levels, around which much of shoreline ecology once revolved. At the end of this chapter there is a long treatment of life cycles and settling behavior. This seems a bit out of place, but the author rightly considers it essential to show how organisms come to arrive on the shore. His practice of going wherever he thinks best within a section makes the book highly readable and personal, but is also one of the large weaknesses, as shown below.

In the next chapter, Carefoot discusses modern ideas of vertical distribution. As a base he uses Connell's idea that upper vertical limits are determined by physical factors and that lower limits are a product of biological processes such as predation. This framework is then expanded, and there are treatments of the various physical factors, and of predation and competition, herbivory, and the keystone predator concept of Paine. Carefoot then proceeds to a consideration of intertidal communities as whole systems in chapter 5, which deals with primary production and its fate, secondary production, and food webs. In this chapter there is also some evolutionary ecology, e.g. "the evolution of a feeding strategy."

The outline is an exciting one. Carefoot draws on many sources for his material and while his coverage is by no means complete or even nearly so, he seems to have touched most of the bases. He doesn't hesitate to go down into the subtidal or off to Nova Scotia for relevant material, and he stretches his outline to accommodate whatever logical destination he thinks to be appropriate. Furthermore, he has no hesitation about being speculative, usually making it clear that he is doing so. Although the tone varies a bit throughout the text, the book will be of interest to people at many levels. I'm sure that it could find use as a supplementary text in ecology courses, also an introduction to the field for researchers; I know that at least one high school class is using it.

The book has problems that will limit its use as a formal text. Carefoot occasionally refers to "ecologists" as if he were setting himself apart from them, and he gives ecologists good reason to welcome this arrangement. The first problem is that the tendency to follow whatever his thoughts lead has left some of the book hopelessly disorganized. In the section called "the upper limits of distribution: light," we find coverage of green algal symbionts in sea anemones, and the effect of light on the *lower* limits of seaweeds. In

a section called "the lower limits: competition between species," we find him instead discussing competition as it affects limits along *horizontal* gradients. This is followed by several pages dealing with competition within a species, having no relation to lower limits of distribution. All this material is interesting, but totally irrelevant to the point that Carefoot purports to be making and hence it will be highly confusing to the student.

The student will be confused further by the frequent instances in which Carefoot arrives at contradictions or dead ends. The section in which he discusses light as a factor determining upper limits ends with the conclusion that light is not important in setting upper limits. He describes Dayton's study of competition between mussels and *Postelsia*, (p. 81) which concludes that log damage prevents competitive exclusion from taking place; then in the very next paragraph tells the reader that this has been an example of the principle of competitive exclusion. Despite citing three studies showing that removal of sea urchins results in downward extension of the range of seaweeds, he concludes that "in no case is it clear that sea urchins set the lower limits of distribution on any species of alga in the subtidal habitat . . ." (p. 103). In chapter 5, Carefoot makes the interesting suggestion that carbon monoxide in *Nereocystis* floats is a defense against herbivores; after half a page of discussion he concludes that it probably isn't. He spends nearly three pages working from theoretical grounds to predict the diet of whelks in the field, then finds it unsupported by the evidence. This is followed right away by an analysis of where whelks locate boreholes when drilling mussels, which concludes that the mystery is still half-solved. But ". . . such is the stuff of research, and research into the biology of an organism very often raises more questions than it answers." (p. 132). This sort of presentation will certainly raise questions in the minds of students, who will wonder what he was saying.

Last in the list of problems are some mistakes. On p. 86 the figure doesn't agree with what the text says. On p. 83 is a more serious error, in which the author brings up the term "population," but doesn't make it clear that he means a statistical population, not a biological one; then he confuses the percentage of overlap of two species on a transect with a statistical percentage, a probability. On p. 89 is a biological mistake, in which it is wrongly assumed that the relations between the barnacles *Chthamalus* and *Balanus* are the same here as in Scotland. If the book is assigned to students, as I have no doubt it will be, some professorial guidance will be required.

In part of the section on mariculture, the book becomes nearly incoherent. Carefoot raises an objection to the destruction of sea urchins with hammers to promote kelpbed growth, which could be a highly tenable position. But the best that can be mustered is that "the act seemed ignoble to the cause." (p. 159). This is followed with a motherhood statement about human interference in nature often turning out wrong, even though the sea urchin smashing project turned out exactly the way it was planned. A few pages later, there is a similar objection to the lobster transplant project carried out by the Fisheries Research Board of Canada. Although this also could have been a reasoned argument with scientific merit, the best we find are sophisms: there is a list of the organisms that were accidentally introduced with oysters and a study is cited showing that lobsters would be detrimental to two species that don't occur in B.C. I don't defend the lobster transplant, but I think that Carefoot's illogical arguments, and the unfair attack on those who carried out the project, reflect badly on the rest of the book. The remaining parts of this chapter and the two that follow contain very little that cannot be found elsewhere.

Despite its flaws, the book (especially the central part) is worth reading for both students and workers in the field. If it stimulates someone to produce the book we're waiting for, it will have done its job.

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(R204)

Energy Flow – Its Biological Dimension. A Summary of I.B.P. in Canada, 1964–1974. *Edited by T. W. M. Cameron and L. W. Billingsley Published for the Canadian Committee of the I.B.P. by the Royal Society of Canada, Ottawa, Ont., 1975. x + 319 p. $5.00.*

In reviewing a book arising out of the International Biological Programme, one is immediately tempted to revive half-forgotten and often acrid arguments as to the purpose and value of this exercise in Big Biology. The I.B.P. was initiated in the first half of the sixties as the biologists' reply to the International Geophysical Years that have proved to be of such value to geophysicists both from the information gathered and in improved public awareness of the science, its problems, and methods. In stimulating awareness of biological problems in the general public, the I.B.P. was a failure; the press was almost nonexistent and even among biologists, one could never be sure that the letters I.B.P. would be understood. It is perhaps the misfortune of the program that it was overtaken and lost sight of among the numerous and very vocal "save our ecology" groups that suddenly flourished during the same period. It is equally unfortunate that, in the public mind, the only thing we now have to do to "regain our ecology" is to pick up our cans and bottle tops. That the intricacies of the real biological world go much deeper than this is fully apparent in the pages of this summary volume of Canada's participation in the program.

As is to be expected, some of the contributions to *Energy Flow – Its Biological Dimensions* are outstanding and of others, one wonders how they came to be included except for the sake of completeness. The great value of the book is that it provides an exciting panoramic view of ecological work in Canada; in a sense it is an ecological text in that it covers a great deal of ground, but with a freshness that comes from individuals reporting on the labors in their own particular vineyard. Many of the major Canadian biomes are represented, from the arctic to the Great Plains, from Georgia Strait to St. Margaret's Bay. That a number of these programs have been an outstanding success is a tribute to the project directors who guided, nursed, and cajoled both those with their hands on the money-tap and those working alongside them in the field. In some cases, merely to get the project into operational status was a great feat; then to direct and extract information of scientific worth was an even greater one. *E pluribus unum* seems to have little significance for the working biologist.

It is to be hoped that the publication of this book will break down some of the barriers existing between various subdisciplines in ecology; do plant ecologists have a message for their animal counterparts, is grazing by animals on the plains of Saskatchewan comparable to grazing by zooplankters on phytoplankton? As may be expected in a compendium of this sort, the results are uneven, varying from what appear to be hurried extracts from an annual report to major efforts to summarize and synthesize a large number of interacting subprojects. It is in this field of synthesis that the major projects have been largely successful and the lines of energy flow delimited; the projects that deserve particular mention in this respect are the studies of production and grazing in the Truelove Lowlands of Devon Island in the high arctic and at the other extreme, production and grazing at Matador on one of the few remaining areas of indigenous prairie grassland. In the aquatic field the studies at Char Lake, again in the high arctic, St. Margaret's Bay, Nova Scotia, the Gulf of St. Lawrence, and the Strait of Georgia between Vancouver and Vancouver Island all deserve very close attention and provide considerable insight into how the system works. However, in each case in spite of resources that are unlikely to be available on such a scale for some time to come, the results are somewhat tentative and subject to great variation. It seems most important at this point that we ask ourselves whether we are asking the right questions and what degrees of precision can we rightly expect even with unlimited effort; are we in fact trying to define the virtually indefinable; how do we extract the major trends and tendencies to achieve a working understanding of a system?

To determine the major conclusions reached by the I.B.P. throughout the world, one naturally turns first to the synthesis of Mann and Brylinsky. Their results are interesting but full of surprises: latitude, for instance, was found to be one of the most reliable abiotic variables with which to predict phytoplankton production. Presumably latitude is not a factor to which plants respond; it is more likely to be the total availability of solar energy, although it has been suggested that this is not necessarily a maximum at the equator on account of cloud cover. Also contrary to expectations is that the effects of latitude override those of nutrients or lake morphology, but as the authors point out, in the latter case it means only that the mean depth and closely related factors such as surface area and volume are not good indices of primary productivity. The next stage would surely be to examine closely within-latitude differences. There appears to be momentary confusion in this section with respect to the significance of the production biomass ratio in that P:B ratio is equated with turnover time whereas turnover time is dimensionally equivalent to the reciprocal of P:B: the smaller the P:B ratio the longer the time of turnover.

The conclusion of Mann and Brylinsky that turnover time increases with latitude is of great interest in that it implies that biomass per unit energy input increases as one proceeds north or south from the equator. Parsons' conclusion (from the Strait of Georgia project) that the harvestable biomass of a terminal predator is greater in a short food chain than in a longer one is a very reasonable view considering the high energy expenditure necessary to convert tissue from one trophic level to another. When this is combined with Rigler's (Char Lake) evidence that food webs simplify and become shorter with increasing latitude it is possible to gain some insight into why the P:B ratio decreases toward the poles. It would also appear that it is in ecosystems where the energy entrained is retained within the system and does not "escape" through migration or predation, that such conditions apply.

In another area of theory, Rigler has driven one more nail into the coffin of the dying but by no means dead hypothesis that diversity engenders ecosystem stability. Few systems that have been measured seem to have less fluctuation than the zooplankton of Char Lake, and few systems described have less species richness.

In yet another theoretical arena there is stimulus for thought: why do terrestrial grazers consume such a small fraction of the food resources that appear to be readily available? In the grasslands of Matador (Coupland, Willard, Ripley, and Randall) a mere 2.6% of the assimilated energy passes through invertebrates and somewhat surprisingly small-mammal grazing is almost insignificant. Even when the grasslands are managed, livestock consume only about 7% of shoots produced. Studies of the terminal predator in Char Lake, however, indicate that a much closer balance between prey and predator exists. Total production of food items is only about 1.4 times the ingestion rate of the char, which, as Rigler points out, "allows for little mortality of prey species other than that due to the char."

A prime candidate for a Guinness Book of Biological Records, were one to be started, would surely be the gymnostomatous pteropod mollusc *Clione* in St. Margaret's Bay. It feeds exclusively on the thecostomatous pteropod *Spirotella retroversa*; as if this were not sufficiently exceptional, it is apparently able to assimilate 90% of that which is ingested and can convert more than 60% of this to new tissue. This exceeds the not inconsiderable ability of the spiders at Matador that convert 28% of grasshopper tissue to that of spider tissue. These values are far above the 10% rates of conversion considered to be about the average value by Mann and Brylinsky.

Whether these rates by themselves can be considered to be ecologically efficient is doubtful; overall ecological efficiency is perhaps better measured by the relationship between energy assimilated and biomass maintained. Such considerations lead to the question as to whether too much emphasis is placed on production in our ecological studies in the same way that economists overemphasize growth. Throughout much of the I.B.P. there has been the further emphasis on measuring production with the implication that it is "production in the service of man." And it is in this aspect that the program has been least satisfactory; only lip service has been paid to the role of man in the multiplicity of ecosystems that he now inhabits.

The section on human adaptability begs the question and concentrates on physiological aspects of ecology. I suspect that this is a compromise between those who regard man as a medium-sized rather aggressive omnivore, who is rapidly changing most of the world's ecosystems to his immediate gain in biomass and those who take the opposite stance that man is in a position aloof from the biological consequences of his actions. Whatever the reasons, the results discussed tend to set apart the functions of man in any ecosystem. While some of the problems investigated are doubtless of great interest in their own right, little of interest is passed on as to the nature, scope, and conclusions of the investigations. One exception is the discussion on the relationship between the Igloolik Inuit community and the parasites of Arctic char (Jamieson and Freeman), one of their staple foods; for a direct approach to a problem this would be difficult to improve upon. At the other extreme is a sociological study that I find completely incompre-

hensible; a conclusion is reached that "reemphasizes the need for careful attention to the construct validity of psychological tests used in cross-cultural context. For example, for the Eskimo all of the sub-tests of the well-known Progressive Matrices seem to tap inductive reasoning from nonverbal skills; but for Nsenga subtests A and B load on field-independence and B, C, D and E on v:ed." Does this just mean that Inuit children engage the mind in gear before putting their mouths in motion? Such encouraging signs are in fact readily apparent in Inuit communities.

In general, however, the writing is good and the book makes for most interesting reading. More editorial insistence on standardization of notations could have been applied with advantage; for example, it is not readily apparent in the paper on the Truelove Lowlands whether assimilation is being measured in terms of O_2 or CO_2.

There is one aspect of the book that I can only interpret as a tribute to that great ecologist Charles Darwin. Darwin, we are told, had little regard for the aesthetics of the book binding and used to dismember even his most valuable books in order that they might be read in comfort in the reclining position. "Energy Flow" improves on this and includes a self-destruct mechanism in the form of a perforation along the spinal margin of each page, that does not allow even a single reading without the book falling to pieces. So emulate the master, tear the book apart, staple the individual papers together, recline, and cogitate for there is much food for thought.

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Books Received/Livres reçus

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Aquacultural Engineering. *Frederick W. Wheaton. John Wiley and Sons, New York, N.Y., 1977. xx + 708 p. $36.00.* (A massive basic text in two parts: Part I covers basic biophysical and biochemical factors in aquaculture, while Part II deals with aquaculture system engineering.)

Modern Deep Sea Trawling Gear. *John Garner. Fishing News Books Ltd., Farnham, Surrey, England, 1977. 83 p.* (A small, well-illustrated manual on Atlantic deep-sea trawling gear.)

Pollutant Effects on Marine Organisms. *Edited by C. S. Giam. Lexington Books, D. C. Heath and Company, Lexington, Mass., 1977. xi + 213 p. $17.00.* (The proceedings of a workshop held on May 16–19, 1976 at Texas A&M University, College Station, Texas, to report on the progress of ongoing research and make recommendations for future programs.)

Trading Off Environment, Economics, and Energy. *Peter W. House. Lexington Books, D. C. Heath and Company, Lexington, Mass., 1977. xix + 135 p. $17.00.* (The subtitle of the book is "EPA's Strategic Environmental Assessment System," which says it all.)

The Economics of Offshore Oil and Gas Supplies. *Frederik W. Mansvelt Beck and Karl M. Wiig. Lexington Books, D. C. Heath and Company, Lexington, Mass., 1977. xiii + 150 p. $17.00.* (A summary of the massive Arthur D. Little, Inc. study of offshore hydrocarbon resources conducted for the U.S. Department of the Interior.)

Middle Eocene Freshwater Fishes of British Columbia. *Mark V. H. Wilson. Life Sciences Contributions No. 113, Royal Ontario Museum, Toronto, Ont. 1977. 61 p. $3.00.* (A soft-cover publication, based on a Doctoral Thesis submitted to the University of Toronto.)

COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

Chemical and sensory analysis of ungutted offshore (nonspawning) capelin (*Mallotus villosus*) stored in ice — **J. R. Botta, P. B. Noonan, and J. T. Lauder**

Diel food selection by two sizes of rainbow trout (*Salmo gairdneri*) in an experimental stream — **P. A. Bisson**

Elevated heavy metals: a stress on a population of white suckers, *Catostomus commersoni*, in Hamell Lake, Saskatchewan — **G. A. McFarlane and W. G. Franzin**

Acceptability of rapeseed proteins in diets of rainbow trout (*Salmo gairdneri*) — **M. Yurkowski, J. K. Bailey, R. E. Evans, J.-A. L. Tabachek, and G. B. Ayles**

Fecundity changes in exploited populations of lake whitefish (*Coregonus clupeaformis*) and lake trout (*Salvelinus namaycush*) — **M. C. Healey**

Notes

Distance chemoreception and vision in the selection of prey by American lobster (*Homarus americanus*) — **R. W. M. Hirtle and K. H. Mann**

Ionization of ammonia in seawater: effects of temperature, pH, and salinity — **C. E. Bower and J. P. Bidwell**

Ammonia quotient in sockeye salmon (*Oncorhynchus nerka*) — **M. N. Kutty**

Perspective

Management alternatives and strategic planning for Canada's fisheries — **W. F. Sinclair**

The need for human sciences research in Atlantic coast fisheries — **R. R. Andersen**

The number following each title in each series refers to the establishments listed at the end of the section.

Les nombres qui suivent les titres de chacune des séries désignent les établissements suivants à la fin de la section.

Recent Studies

Until 1970, reprints of these articles had been included in an annual volume of "Studies," composed of two parts. The final binding was the 1969 Studies, Part 2, which included No. 1355. These are no longer bound and distributed. We continue, however, to number and list all articles on investigations published in other periodicals, which henceforth may be obtained in reprint form only from the author or originating establishment.

Récentes études

Jusqu'en 1970, ces articles étaient réimprimés, puis reliés dans un volume annuel d'études, comprenant deux parties. Les études de 1969, partie 2, incluant le n°1355, ont été les dernières à être reliées. Nous n'en faisons désormais plus la reliure ni la distribution. Nous continuons cependant de numéroter les articles et d'en établir des listes d'études sur des recherches mentionnées dans d'autres périodiques. On peut donc se les procurer, sous leur forme réimprimée seulement, de l'auteur ou du service dépositaire.

2466. WILDISH, D. J. 1977. Factors controlling marine and estuarine sublittoral macrofauna. Helgol. Wiss. Meeresunters. 30: 445–454. (6)

2467. CONOVER, R. J., AND M. A. PARANJAPE. 1977. Comments on the use of a deep tank in planktological research. Helgol. Wiss. Meeresunters. 30: 105–117. (7)

2468. CASTELL, J. D. 1977. Production of juvenile lobsters (*Homarus americanus*) for nutrition research. p. 277–281. *In* 3rd Meeting of the I.C.E.S. Working Group on Mariculture, Brest, France. May, 1977. (8)

2469. CLARKE, W. C., S. W. FARMER, AND K. M. HARTWELL. 1977. Effect of teleost pituitary growth hormone on growth of *Tilapia mossambica* and on growth and seawater adaptation of sockeye salmon (*Oncorhynchus nerka*). Gen. Comp. Endocrinol. 33: 174–178. (1)

2470. CLARKE, W. C., AND Y. NAGAHAMA. 1977. Effect of premature transfer to sea water on growth and morphology of the pituitary, thyroid, pancreas, and interrenal in juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Zool. 55: 1620–1630. (1)

2471. LUDWIG, B., D. A. HIGGS, U. H. M. FAGERLUND, AND J. R. MCBRIDE. 1977. A preliminary study of insulin participation in the growth regulations of coho salmon (*Oncorhynchus kisutch*). Can. J. Zool. 55: 1756–1758. (3)

2472. KABATA, Z., AND S. N. WILKES. 1977. *Peniculus asinus* (Copepoda: Pennellidae), a new species of copepod parasitic on fishes of the genus Sebastes along the west coast of North America. Can. J. Zool. 55: 1988–1991. (1)

2473. VANBREE, P. J. H., D. E. SERGEANT, AND W. HOEK. 1977. A harbour porpoise, *Phocoena phocena* (Linnaeus, 1758), from the Mackenzie River delta, Northwest Territories, Canada. (Notes on cetacea, delphinoidea VIII). Beaufortia Ser. Misc. Publ. Zool. Mus. Univ. Amsterdam 26: 99–105. (5)

2474. CROSS, T. F., AND R. H. PAYNE. 1977. NADP-isocitrate dehydrogenase polymorphism in the Atlantic salmon *Salmo salar*. J. Fish. Biol. 11: 493–496. (9)

2475. BEVERLY-BURTON, M., AND J. H. C. PIPPY. 1977. Morphometric variation among larval *Anisakis simplex* (Nematoda: Ascaridoidea) from fishes of the north Atlantic and their use as biological indicators of host stocks. Env. Biol. Fish. 2: 309–314. (9)

2476. KEIZER, P. D., J. DALE, AND D. C. GORDON JR. 1978. Hydrocarbons in surficial sediments from the Scotian Shelf. Geochim. Cosmochim. Acta. 42: 165–172. (7)

2477. KE, P. J., D. M. NASH, AND R. G. ACKMAN. 1977. Mackerel skin lipids as an unsaturated fat model system for the determination of antioxidative potency of TBHQ and other antioxidant compounds. J. Am. Oil Chem. Soc. 54: 417–420. (8)

2478. MAYZAUD, P., AND R. G. ACKMAN. 1978. The 6,9,12, 15,18-Heneicosapentaenoic acid of seal oil. Lipids 13: 24–28. (8)

2479. ACKMAN, R. G., AND C. A. EATON. 1978. Some contemporary applications of open-tubular gas–liquid chromatography in analyses of methyl esters of longer-chain fatty acids. Fette. Seifen. Anstrichm. 80: 21–37. (8)

2480. ZITKO, V. 1978. Nonachlor and chlordane in aquatic fauna. Chemosphere 1: 3–7. (6)

2481. FLANNAGAN, J. F. 1978. The winter stoneflies *Allocapnia granulata* (Taeniopterygidae), *Taeniopteryx nivalis* and *T. parvula* (Capniidae) in southern Manitoba. Can. Entomol. 1: 111–112. (4)

2482. AYLES, G. B., AND J. BARICA. 1977. An empirical method for predicting trout survival in Canadian prairie lakes. Aquaculture 12: 181–185. (4)

2483. KLAVERKAMP, J. F., M. DUNGSAWASDI, W. A. MACDONALD, AND H. S. MAJEWSKI. 1977. An evaluation of fenithrothion toxicity in four life stages of rainbow trout, *Salmo gairdneri*. Am. Soc. Test. Mater. Spec. Tech. Publ. 634: 231–240. (4)

2484. VERMEER, K., AND C. D. LEVINGS. 1977. Populations, biomass and food habits of ducks on the Fraser Delta intertidal area, British Columbia. Wildfowl 28: 49–60. (3)

2485. NEWBURY, R. W., AND K. G. BEATY. 1977. Water budgets in small precambrian lake basins in northwestern Ontario, Canada. p. 132–139. *In* Proc. 2nd Conf. on Hydrometeorology, Toronto, Ont., October 1977. (4)

2486. WALLACE, R. R. 1977. A discussion on the use of behaviour by *Gammarus pseudolimnaeus* Bousfield in evaluating environmental stress. p. 59–67. *In* Proc. 3rd Aquatic Toxicity Workshop, Halifax, N.S., November 1976. (4)

Technical Report Series

Technical Reports are research documents that are of sufficient importance to be preserved, but which for some reason are not appropriate for primary scientific publication. *Inquiries concerning any particular Report should be directed to the issuing establishment.*

730. ROGER, I. H., AND H. W. MAHOOD. 1977. The use of a macroreticular resin in the analysis of kraft pulping effluents for resin acids. 13 p. (1)

731. WOJTOWICZ, M. B., M. G. FIERHELLER, R. LEGENDRE, AND L. W. REGIER. 1977. A technique for salting lean minced fish. 15 p. (8)

Rapports techniques

Les rapports techniques sont des documents de recherche qui revêtent une assez grande importance pour être conservés mais qui, pour une raison ou pour une autre, ne conviennent pas à une publication scientifique de fonds. Pour toute demande de renseignements concernant un rapport particulier, il faut s'adresser au service responsable.

732. DONALDSON, E. M. 1977. Bibliography of fish reproduction 1963–1974. Part 1: General, non-teleostean species and Teleostei, Abramis to Clinostomus. Part 2: Teleostei, Clupea to Ompok. Part 3: Teleostei, Oncorhynchus to Zygonectes and Addendum. 571 p. (3)

Interpretive Articles Series

This new series commenced in 1966. The articles interpret work already published in primary journals. They appear at irregular intervals in various technical publications. Frequently an article essentially duplicates, condenses, or is based on an article in another series.

392. MANSFIELD, A. W. 1974. Methods of assessing seal populations in the Baltic. p. 79–100. *In* Proc. Symp. on the Seal in the Baltic, Lidingo, Sweden, June, 1974. 26 p. (5)

393. GERACI, J. R., AND T. G. SMITH. 1977. Consequences of oil fouling on marine mammals, p. 399–410. *In* Effects of petroleum on arctic and subarctic marine environments and organisms. Vol. 11. Academic Press, Inc., New York, N.Y. (5)

394. SMITH, T. G. 1978. Travelling the arctic by snowmobile. Can. Geogr. J. Feb./Mar., 1978: 60–65. (5)

Articles explicatifs

Cette série a débuté en 1966. Les articles donnent une explication de travaux déjà publiés dans des revues prioritaires. Ils paraissent à intervalles irréguliers, dans diverses publications techniques. Souvent, un article se basera sur un écrit d'une autre série, le condensera ou le reproduira *presque tel quel.*

395. MITCHELL, E. D. 1974. Endangered whales in waters off Canada, p. 162–164. *In* D. Stewart [ed.] Canadian endangered species. Gage Publishing Ltd., Toronto. (5)

396. SERGEANT, D. E. 1978. Book review of: F. Bruemmer, 1978. The life of the harp seal. Can. Geo. J. 96: p. 76. (5)

397. DAVIS, J. C. 1974. Bioassay procedures and sublethal effect studies with full bleached kraft mill effluent and Pacific salmon. Pulp Pap. Mag. Can. July: 1–4. (3)

Manuscript Reports

This series includes unpublished preliminary reports and data records not intended for general distribution. They should not be referred to in publications without clearance *from the issuing establishment and without clear indication* of their manuscript status.

1430. HAEGELE, C. W., AND M. J. HAMEY. 1977. Shoreline vegetation maps of some major herring spawning localities on the west coast of Vancouver Island: Nuchatlitz, Nootka Sound, Hesquiat Harbour, and Barkley Sound. 41 p. (1)

1431. CADDY, J. F., T. AMARATUNGA, M. J. DADSWELL, T. EDELSTEIN, L. E. LINKLETTER, B. R. MCMULLIN, A. B. STASKO, AND H. W. VAN DE POLL. 1977. 1975 Northumberland Strait project, part I: Benthic fauna, flora, demersal fish, and sedimentary data. 46 p. (6)

1432. STASKO, A. B., T. AMARATUNGA, AND J. F. CADDY. 1977. 1975 Northumberland Strait project, part II: Commercial shell fish data. 29 p. (6)

Rapports manuscrits

La série comprend des articles d'information et des rapports préliminaires non publiés, qui ne sont pas destinés à la distribution générale. Ils ne doivent pas être donnés en références sans l'assentiment du service dépositaire et sans une indication claire de leur forme manuscrite.

1433. HAEGELE, C. W. 1977. Vegetation survey of herring spawning localities in Ganges Harbour, B.C. 17 p. (1)

1434. GLOVA, G. J., AND J. C. MASON. 1977. Comparison of coastal cutthroat trout populations in allopatry and those sympatric with coho salmon and sculpins in several small coastal streams on Vancouver Island, B.C. 35 p. (1)

1435. ADKINS, B. D., AND A. P. STEFANSON. 1977. An examination of harvested and unharvested abalone populations in the Moresby Island area. 23 p. (1)

Data Reports

These reports provide a medium for filing and archiving *data compilations where little or no analysis is included.* Such compilations commonly will have been prepared in support of other journal publications or reports. The subject matter of Data Reports reflects the broad interests and policies of the Fisheries and Marine Service, namely, fisheries *management, technology and development, ocean sciences* and aquatic environments relevant to Canada.

Numbers 1–25 in this series (except No. 24 issued by Newfoundland Region, St. John's, Nfld.) were issued as Fisheries and Marine Service Data Records by the Pacific Biological Station, Nanaimo, B.C. The series name was changed with report number 26.

Rapports statistiques

Ces rapports servent de base à la compilation des données de classement et d'archives pour lesquelles il y a peu ou point d'analyse. Cette compilation aura d'ordinaire été préparée pour appuyer d'autres publications ou rapports. Les sujets des Rapports statistiques reflètent la vaste gamme des intérêts et politiques du Service des pêches et de la mer, *notamment gestion des pêches, techniques et développement,* sciences océaniques et environnements aquatiques, au Canada.

Les numéros de 1 à 25 de cette serie (sauf le nº 24, publié par région de Terre-Neuve, St-Jean, T.-N.) ont été publies à *titre de Records statistiques, Service des pêches et de la* mer, par la Station biologique de Pacifique, Nanaïmo, (C.-B.). Le nom de la série a été modifie à partir du numéro 26.

41. WASCASEY, J. W., E. G. ATKINSON, L. DERICK, AND A. WEINSTEIN. *1977. Zoobenthos data from the southern* Beaufort Sea, 1971–1975. 187 p. (5)

42. HARLING, W. R., AND D. DAVENPORT. 1977. *G.B. REED* Groundfish Cruise No. 77-3, August 22 to September 8, 1977. 46 p. (1)

Industry Reports

These reports contain the results of research and development that are useful to industry for either immediate or future application. Industry Reports are directed primarily *towards individuals in the primary and secondary sectors of* the fishing and marine industries. No restriction is placed on subject matter and the series reflects the broad interests and policies of the Fisheries and Marine Service, namely, fisheries management, technology and development, ocean sciences and aquatic environments relevant to Canada.

Industry Reports may be cited as full publications. The correct citation appears above the abstract of each report. Each report will be abstracted in *Aquatic Sciences and Fisheries Abstracts* and will be indexed annually in the Service's index to scientific and technical publications.

Numbers 1–91 in this series were issued as Project Reports *of the Industrial Development Branch, Technical Reports of* the Industrial Development Branch, and Technical Reports of the Fisherman's Service Branch. The series name was changed with report number 92.

Rapports à l'industrie

Ces rapports contiennent les résultats des recherches et des progrès pouvant être utiles à *l'industrie pour des applications* soit immédiates, soit futures. Ils sont principalement préparés *à l'intention des membres des secteurs primaire et secon*daire de l'industrie des pêches et de la mer. Il n'y a aucune restriction quant au sujet; de fait, la série reflète la vaste gamme des intérêts et des politiques du Service des pêches et de la mer, notamment: la gestion des pêches, les tech*niques et la mise en valeur, les sciences océaniques et l'en*vironnement aquatique au Canada.

Les Rapports à l'industrie peuvent être considérés comme des publications complètes. La titre exact paraît au haut du résumé de chaque rapport devant être publié dans la revue *Aquatic Sciences and Fisheries Abstracts et noté dans l'index* annuel des publications scientifiques et techniques du Service.

Les numéros 1 à 91 de cette série ont été publiés à titre de rapports sur les travaux de la Direction du développement industriel, de rapports techniques de la Direction du développement *industriel, et de rapports techniques de la Direction* des services aux pêcheurs. Le nom de la série a été changé à *partir du rapport nº 92.*

93. CAUVIN, D. M., AND P. C. THOMPSON. *1977. Rainbow* trout farming: An economic perspective. 24 p. (4)
94. *WESTRHEIM, S. J. 1977. Production and stock assess*ment of principal groundfish stocks off British Columbia. *77 p. (1)*
95. TAYLOR, A. R. A. 1975. Studies of the *Gracilaria* community in Hill river, Prince Edward Island. 38 p. (10)
96. TAYLOR, *A. R. A. 1975. Phototransect studies of Chondrus communities in the maritime provinces. 34 p.* (10)
97. WANG, J. C. C., AND E. R. AMIRO. 1977. Cold storage of the American oyster (*Crassostrea virginica*) in the shell. 23 p. (8)
98. DUNN, D. L. *1977. Canada's east coast sealing industry* 1976: A socioeconomic review. 54 p. (10)

Translation Series

The following translations have been prepared by or for the Fisheries and Marine Service, for use in its investigations. Copies are available from Translation Services, Canada Institute for Scientific and Technical Information, National Research Council of Canada, Ottawa, Ontario K1A 0S2, at a cost of 22¢ per page and a minimum charge of $2.20. Information on translations can be obtained from the Scientific Information and Publications Branch.

Traductions

Les traductions dont il est question ci-après ont été préparées par ou pour le Service des pêches et des sciences de la mer, à des fins de recherche. On peut en obtenir des exemplaires, à 22¢ la page et à un prix minimum de $2.20 aux Services de traduction, Institut canadien de l'information scientifique et technologique, Conseil national de recherches du Canada, Ottawa (Ontario), K1A 0S2. La Direction de l'information et des publications scientifiques peut fournir des renseignements sur ces traductions.

TAGLIAMONTE, B., AND G. TOMASSI. 1976. Odd-numbered carbon atom fatty acids: metabolic and nutritional aspects. Riv. Sci. Tec. Aliment. Nutr. Umana 6: 7–12. (Transl. from Italian by Fish. Mar. Serv. Transl. Ser. No. 4164, 1977)

KOPPEL, Z., AND J. KOCIS. 1974. Hemolytic activity of *Aeromonas hydrophila* and some properties of isolated hemolysins. Folia Vet. 18: 614–635. (Transl. from Slovak by Fish. Mar. Serv. Transl. Ser. No. 4165, 1977)

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BAUER, O. N., A. V. GUSEV, AND V. A. ROITMAN. 1976. Results and prospects of investigation into the fauna and systematics of helminths encountered in freshwater fishes of the USSR. Probl. Obshch. Gel'mintol. 26: 125–142. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 4167, 1977)

GUKALOVA, T. P., V. S. KOZLOVA, V. A. BUZINA, A. P. KRASNOSHCHEK, AND T. P. MEDVEDEVA. 1974. Gas chromatographic analysis of isovaleric acid esters. Dostizh. Razvit. Nov. Metodov Khim. Anal. p. 3–4. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 4168, 1978)

TSUKUDA, N. 1977. Changes in the lipids of frozen fish. II. Changes in the lipids of chum salmon and cod muscle during frozen storage. Tokai-ku Suisan Kenkyusho Kenkyu Hokoku (89): 1–6. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 4169, 1977)

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BIEDERMANN, R., A. L. PRABUCKI, AND H. VOGTMANN. 1977. The nutritive physiological action of rapeseed oils of various origins. Mitt. Geb. Lebensmittelunters. Hyg. 68: 100–111. (Transl. from German by Fish. Mar. Serv. Transl. Ser. No. 4176, 1978)

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ORLOV, YU. E., G. I. YADYKIN, V. T. VERTUSHKOV, AND I. A. UDALOV. 1975. The chemical composition of sperm oil. Sb. Nauchn. Tr. Ryazan. Med. Inst. (50): 30–35, 58–63. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 4178, 1978)

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ANNOUNCEMENTS / AVIS

Second International Atlantic Salmon Symposium

The symposium will be held on September 26–28, 1978 at the University of Edinburgh, Edinburgh, Scotland. It is sponsored by the Atlantic Salmon Research Trust, Ltd. and the International Atlantic Salmon Foundation. If there is sufficient demand IASF hopes to arrange a return air charter to Edinburgh.

The theme of the symposium will be "The Atlantic salmon in the world of tomorrow" and the papers (invited) will deal with current topics in management and research. Five sessions are planned. These will include an overview of Atlantic salmon resources and developments in international law, conflicts in salmon exploitation, ecology and management, Atlantic salmon cultivation, and an overview of future changes and prospects for world Atlantic salmon resources.

For preliminary registration (discounted to approximately $65) and additional details please contact

The International Atlantic Salmon Foundation
P.O. Box 429
St. Andrews, New Brunswick, Canada
E0G 2X0
Telephone (506) 529-3818 or 529-3293

Deuxième colloque international sur le saumon atlantique

Ce colloque se tiendra à l'Université d'Edinbourg, Edinbourg, Écosse, du 26 au 28 septembre 1978. Il est organisé par l'Atlantic Salmon Research Trust, Ltd. et la Fondation internationale du saumon atlantique. Si la demande le justifie, la FISA espère organiser un vol d'affrètement aller–retour à Edinbourg.

Le colloque aura pour thème : « Le saumon atlantique dans le monde de demain », et les travaux (présentés sur invitation) traiteront les sujets d'actualité dans le domaine de la gestion et de la recherche. On prévoit cinq séances. Elles porteront sur une vue d'ensemble des ressources et développements en droit international relativement au saumon atlantique, les conflits dans l'exploitation du saumon, l'écologie et la gestion, la salmoniculture et une vue d'ensemble des changements futurs et des perspectives d'avenir en ce qui a trait aux ressources mondiales de saumon atlantique.

On pourra s'enregistrer à l'avance (au taux réduit d'environ $65) et obtenir des détails supplémentaires en s'adressant à

La Fondation internationale du saumon atlantique
Casier postal 429
St. Andrews, Nouveau-Brunswick, Canada
E0G 2X0
Téléphone (506) 529-3818 ou 529-3293

Third International Congress on the History of Oceanography

Call for Papers and Expressions of Interest

The Third International Congress on the History of Oceanography will be held at Woods Hole, Massachusetts, U.S.A., September 22–26, 1980. As part of the celebration of the 50th anniversary of the Woods Hole Oceanographic Institution, the Congress will be followed the next week (Sept. 29–Oct. 4) by an Assembly on current and future oceanography.

The Congress has the approval of both the International Union of History and Philosophy of Science and the Centre International d'Histoire de l'Océanographie.

Expressions of interest in this Congress, particularly from those who plan to contribute papers on any aspect of the History of Oceanography, will be most welcome *as soon as possible*. Daniel Merriman, Professor Emeritus of Biology, Yale University, has accepted the Chairmanship and all communications should be addressed to him at

Troisième Congrès International d'Histoire de l'Océanographie

Invitation à présenter des communications ou à *indiquer son intention d'assister*

Le Troisième Congrès International d'Histoire de l'Océanographie se tiendra à Woods Hole, Massachusetts, É.-U., du 22 au 26 septembre 1980. Comme l'un des événements qui marqueront le 50e anniversaire de fondation de la Woods Hole Oceanographic Institution, le Congrès sera suivi la semaine suivante (29 septembre–4 octobre) d'une Assemblée au cours de laquelle on traitera de l'océanographie présente et future.

Le Congrès a reçu l'approbation à la fois de l'International Union of History and Philosophy of Science et du Centre International d'Histoire de l'Océanographie.

Les personnes intéressées à ce Congrès surtout celles qui ont l'intention de présenter des travaux sur tout aspect de l'histoire de l'océanographie sont priées de communiquer *le plus tôt possible* avec le président, M. Daniel Merriman, professeur émérite de biologie, Université Yale, a accepté la présidence du Congrès. Toutes communications devront lui être adressées à

298 Sperry Road
Bethany
Connecticut 06525, USA

Torry Research Station Jubilee Conference

An International Conference on Fish Science and Technology will be held in Aberdeen, Scotland, from July 23 to 27, 1979 in connection with the 50th anniversary of the establishment of the Torry Research Station.

The aims of the Conference are to review the state of advancement in various areas of fish science and technology and to provide a forum for the presentation of the latest findings in research and development. The 15 plenary lectures, given by leading authorities, will combine a retrospective account of developments over the past 50 years with appraisals of the current position and of probable future trends. Time will be available for scientists and technologists to present about 35 papers discussing accounts of original work. The papers will be selected on the basis of interest and topicality. All the lectures and papers will be published.

The Conference will last 4 days in two equal halves separated by 1 day devoted to visits. On this middle day, the Torry Research Station will be open to visitors. Post-Conference tours will be arranged to places of interest.

A brochure giving fuller details and an application form will be available towards the end of 1978 from

Conférence à l'occasion du jubilée de la Torry Research Station

Une Conférence internationale sur la science et la technologie des poissons se tiendra à Aberdeen, Écosse, du 23 au 27 juillet 1979 pour marquer le 50e anniversaire de fondation de la Torry Research Station.

Les buts de la conférence sont de passer en revue l'état actuel de nos connaissances dans les divers domaines de la science et de la technologie des poissons et de fournir aux chercheurs l'occasion de présenter les plus récentes découvertes en recherche et développement. Un regard rétrospectif sur les développements des 50 dernières années sera combiné avec une évaluation de la position présente et des tendances futures probables au cours de 15 conférences pléniaires données par des autorités en la matière. Il y aura du temps de disponible pour permettre aux scientifiques et technologues de présenter environ 35 articles portant sur des travaux originaux. Ces articles seront choisis selon leur intérêt et leur à-propos. Les conférences et les articles seront tous publiés.

La conférence, qui durera 4 jours, sera divisée en deux parties égales séparées par une journée consacrée à des visites. Ce jour-là, la Torry Research Station sera ouverte aux visiteurs. Après la conférence, il y aura excursions à des endroits intéressants.

On pourra se procurer une brochure contenant plus de détails et un formulaire d'enregistrement en s'adressant, vers la fin de 1978, à

Torry Research Station
P.O. Box 31
135 Abbey Road
Aberdeen AB9 9DG Scotland

National Museums of Canada — Invertebrate Collections (Parasites)

The National Museum of Natural Sciences (NMNS) recently appointed, through the courtesy of the Canada Department of Agriculture, Mr W. A. Webster as Honorary Curator of Parasites. The Museum will serve as a permanent repository for protozoan and helminth parasites and this collection will be maintained as a unit within the National Collection of Invertebrates. Material deposited in this collection will be available, subject to certain conditions, to all qualified parasitologists. The NMNS suggests that scientists break up large series, especially type series, so that the various parts may be placed in more than one repository.

Parasitic crustaceans will continue to be part of the Collection of Crustacea of the NMNS rather than of the Parasite Collection. Similarly collections of free-living or plant parasitic nematodes, or ectoparasitic terrestrial arthropods will be maintained at the Biosystematics Research Institute, (K. W. Neatby Building), Agriculture Canada, Ottawa, Ontario K1A 0C6.

Instructions for submission of specimens to the Invertebrate Collection (Parasites) or for obtaining loans of specimens are available from

Invertebrate Collection (Parasites)
Invertebrate Zoology Division
National Museum of Natural Sciences
Ottawa, Ontario, Canada
K1A 0M8

Musées Nationaux du Canada — Collections d'invertébrés (parasites)

Le Musée national des sciences naturelles (MNSN) nommait récemment, à titre gracieux du ministère de l'Agriculture du Canada, M. W. A. Webster comme conservateur honoraire des parasites. Le Musée abritera en permanence la collection de protozoaires et d'helminthes parasites qui sera maintenue comme unité dans la collection nationale d'invertébrés. Tous les parasitologistes qualifiés pourront avoir accès, sujet à certaines conditions, au matériel déposé dans cette collection. Le MNSN suggère aux scientifiques de morceler les grandes séries, surtout les séries types, de façon que les différentes parties soient placées dans plus d'un dépôt.

Les crustacés parasites continueront de faire partie de la collection des crustacés du MNSN plutôt que de celle des parasites. Il en est de même des collections de nématodes libres ou parasites des plantes, ou des arthropodes terrestres ectoparasites qui demeureront à l'Institut de recherche biosystématique, (Immeuble K. W. Neatby), Agriculture Canada, Ottawa, Ontario K1A 0C6.

On pourra se procurer les directives relatives à la soumission de spécimens à la collection d'invertébrés (parasites) ou à l'emprunt de spécimens en s'adressant à

Collection d'invertébrés (parasites)
Division de la zoologie des invertébrés
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Ottawa, Ontario, Canada
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